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held jointly with The Zoological Society of London

Mr. A. D. Cotton, O.B.E., President,
in the Chair.

The Proceedings of the Anniversary Meeting held on Monday, 24 May 943, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the ast meeting :—Dr. T. E. Wallis, Professor F. E. Weiss, The Bentham-Moxon Trustees, U.S. Department of Agriculture and the Royal College f Surgeons of England.

Read for the first time a certificate of recommendation of the following andidate for Fellowship :—Sir Murdoch McLeod, Bt.

The President announced his appointment of Vice-Presidents for 943–4 :—Dr. E. S. Russell, O.B.E., Mr. C. C. Hentschel, Professor F. T. Brooks, F.R.S., and Dr. B. Barnes.

Communications on the taxonomic value of the anatomical features f the vegetative organs of the Dicotyledons were read and discussed :— Dr. C. R. Metcalfe : ‘ An introduction, with special reference to the natomy of the leaf and stem ’. Dr. L. Chalk : ‘ The taxonomic value f wood anatomy ’. Mr. B. J. Rendle : ‘ The rôle of anatomy in the ractical identification of commercial timbers ’. Professor T. M. Harris: Fossil plants ’. Dr. C. Leighton Hare : ‘ The anatomy of the petiole nd its taxonomic value ’. Dr. T. E. Wallis : ‘ The rôle of anatomy n controlling the adulteration of crude drugs ’. Dr. T. A. Sprague ummed up from the point of view of the herbarium botanist.

Dr. Marie Stopes contributed to the discussion ; and the President hanked those who had taken part.

ON THE TAXONOMIC VALUE OF THE ANATOMICAL STRUCTURE OF THE VEGETATIVE ORGANS OF THE DICOTYLEDONS.

1. AN INTRODUCTION, WITH SPECIAL REFERENCE TO THE ANATOMY OF THE LEAF AND STEM.

By C. R. Metcalfe.

Anatomical features of the vegetative organs of the higher plants are of much value in taxonomy when used to supplement those of the external morphology : but a special classification based on anatomical structure alone would possess only limited practical value and not be natural. It follows that for both types of character to be effective close collaboration between anatomists and taxonomists is essential. Hitherto the most frequent emphasis in anatomical work in this country has been on the relationship of structure to physiological function or habitat, rather than on that which exists between anatomy and the generally accepted systems of classification. The taxonomic value of anatomy has been far more widely appreciated on the Continent and in the United States than in this country. One consequence of this has been that taxonomists and those interested in other branches of botany have, until recently, tended to work in watertight compartments. Nowadays it is fortunately becoming more widely appreciated that systems of classification must be based on as many attributes of living organisms as practical experience shows to be reliable, and the barrier between taxonomy and other branches of botany is being broken down, to the mutual advantage of all concerned. Just as taxonomists have learned the value of co-operation from cytologists and geneticists, so are they coming to realize the contributions which anatomists can make.

Practical reasons for using anatomical features.—If the anatomist is to make his contribution to taxonomy, we must first enquire what practical advantages are likely to accrue from his co-operation. The full answer to this question cannot at present be given for the very reason that the anatomy of the higher plants is very imperfectly known from the taxonomic standpoint. Such facts as have been recorded, however, indicate that just as cytological and genetical studies are most valuable in the interpretation of species and subspecific categories of plants, so will anatomical structure, if employed with discretion, provide confirmatory evidence concerning the interrelationships of families or help to establish the correct family positions of genera whose affinities are uncertain. Anatomical characters which serve to distinguish species or groups of less than specific rank are generally of size or frequency rather than kind, features whose significance usually requires to be elucidated by statistical methods requiring much time as well as more material than is often available. Anatomy is, in fact, of most value in the interpretation of genera and families, and sometimes serves to emphasize where groups of families are related to one another. A very large number of instances where anatomy supports one rather than the other of two alternative taxonomic groupings have been noted at Kew during the course of the extensive anatomical survey of the Dicotyledons which is still in progress. Examples could be given if space permitted, but as all of this information will eventually be published in a book, details have been omitted from the present discussion.

Another practical reason for making use of anatomy is because the microscopical features frequently give a clue to the affinities of herbarium specimens which are not accompanied by flowers or fruits. That this can be done has repeatedly been shown at Kew, and the possibilities in this direction will undoubtedly increase as the anatomy of the higher plants becomes more fully known. Particularly valuable results can be obtained with tropical specimens, the flowers of which are often not available or inaccessible on collecting expeditions.

The anatomical method also possesses considerable economic value, since it enables the botanical identity of commercial samples of economic plants, timbers, fibres and other miscellaneous botanical items to be established. Anatomy also proves useful on occasion in helping to establish the guilt or otherwise of suspected criminals. Finally, it may be pointed out that a complete anatomical survey is a necessary preliminary to the interpretation of palaeobotanical remains. From the purely scientific point of view this may prove to be the most interesting aspect of the whole subject.

Technique.—Probably nothing has done more to inhibit the development of systematic anatomy than failure to assemble reference collections of permanent microscopical preparations filed on a taxonomic basis. Collections of this kind are as important for studies in systematic anatomy as are herbarium specimens for all taxonomic work. This has been more fully appreciated by our forestry colleagues than by the general botanist. In consequence we are familiar not only with the fine collections of microscopical slides of timbers which have been assembled at Yale University by Professor S. J. Record, but with those in this country made by Dr. Chalk at Oxford and by Mr. Rendle and his colleagues at Princes Risborough. A similar collection of slides was started more recently at Kew, with, in addition to timbers, many thousands of slides of stems and leaves, special attention having been given to plants and plant products of economic importance. At present there are only some fifteen minor families of Dicotyledons of which no slides have yet been included in the Kew collections. The combined slide collections at the Imperial Forestry Institute, at the Forest Products Research Laboratory and at Kew undoubtedly form a unique assemblage, capable of affording considerable assistance to all who are interested in systematic anatomy.

The exchange and loan of slides between different institutions should be given every encouragement, and will undoubtedly prove to be advantageous to all concerned, just as the corresponding practices with herbarium sheets have proved of very great value in the development of systematic botany in general.

It is perhaps important to emphasize that, although collections of permanent microscope slides are of fundamental importance, they alone will not reveal all of the characters which are of diagnostic value. In many instances it is desirable to supplement the study of permanent mounts by observations on microchemical reactions, macerations and temporary preparations in dilute glycerine, all of which are capable of revealing important features which are not visible in permanent slides.

Characters of taxonomic importance.—Characters must be relatively fixed and non-plastic if they are to possess taxonomic value. Ecological and biological specializations which have arisen in response to peculiarities of environment are of more limited use. Experience alone can indicate which features come into each of these two categories, and it must be clearly understood that similar characters are not necessarily of equal taxonomic significance in all sections of the Dicotyledons. It is well known that the same principle applies when making use of features of external morphology. Furthermore, just as combinations of characters of the external morphology have been found to possess greater taxonomic value than single characters, so the systematic anatomist finds that the co-existence of several characters provides a more reliable basis for identification than any single one. Numerical differences, such as those of variation in frequency, length and so on, should be used with the utmost caution in systematic anatomy, as one frequently finds that apparent distinctions based on such features tend to break down when sufficiently large numbers of samples are examined. One must also point out that the common occurrence of a single character in two plants which are otherwise quite unrelated must not necessarily be taken as an indicator of taxonomic affinity. Parallel development of anatomical similarities has undoubtedly occurred. Nevertheless, features like these possess diagnostic value provided they are of restricted occurrence.

Subject to the above considerations, it may be said that combinations of variations of the following characters are reliable for diagnostic purposes :—

A. Leaf.

1. The diversity of epidermal hairs.
2. Types of stomata. Several types may be recognized, depending on the nature and arrangements of the adjacent subsidiary and epidermal cells.
3. Variations in the size and shape of epidermal cells, as well as the restricted occurrence of vertical and horizontal divisions of the cells.
4. The presence or absence of hypoderm.
5. The structure of the veins, particularly the nature of the cells adjacent to the vascular bundles. It is important to ensure that only veins of the same order are compared.
6. The petiole structure. For further details see Dr. Hare's contribution.

B. Herbaceous stems and young shoots of shrubs and trees.

1. The position of origin of the cork. (The importance of this feature, although often characteristic, has been rather over-emphasized in the past.)
2. The distribution and nature of the pericyclic sclerenchyma.
3. The structure and arrangement of the primary vascular bundles.

(Contrary to the general belief, the degree of separation of the primary vascular bundles is not strictly correlated with the herbaceous or woody habit of the plants. Woody plants with widely separated primary bundles are known to occur, and there are also herbs in which the primary vascular system has the form of a closed ring even when very young.)

4. The occurrence of medullary and/or cortical bundles.
5. Anomalous secondary thickening.

C. Secondary xylem.

Many characters of the secondary xylem are of fundamental diagnostic value. See contributions of Dr. Chalk and Mr. Rendle.

D. Microchemical reactions.

1. Diversity and distribution of different kinds of crystals.
2. The morphology of starch grains.
3. The presence of cystoliths.
4. The laticiferous system, when present.
5. Secretory elements and the nature of their contents.
6. The occurrence of special chemical substances such as berberin or myrosin.

Other characters, such as the occurrence of various kinds of idioblasts or sclerenchymatous elements in the mesophyll, are often of generic or specific diagnostic value, but space does not permit further consideration of other less important characters.

The value of anatomy in phylogenetic studies.—Phylogenetic studies based on comparative anatomy alone are not likely to be more fruitful than similar work which rests solely on comparison of the external morphology of plants which exist at the present day. It is important to avoid making use of preconceived ideas on characters regarded as primitive or advanced respectively without adequate geological evidence. Here we come to the familiar difficulty that the early history of the Angiosperms is so shrouded in obscurity that we are apt to pass easily into the realms of pure speculation. Such geological records as we do possess, however, provide evidence of the contemporary existence of such diverse plants as relatives of the modern genera *Artocarpus*, *Cinnamomum*, *Dalbergia*, *Menispermum* and *Quercus* in the Cretaceous deposits of Greenland, where they occurred very early in the history of the Angiosperms. In the late Cretaceous the diversity of Angiosperms was quite considerable. Such slender evidence as exists rather tends to indicate that the origin of the Angiosperms was no solitary evolutionary event followed by the phylogenetic development of the modern Angiosperms from a single prototype. The polyphyletic origin of the Angiosperms tends to be supported by the fact that we do not find all the characters which are generally believed to be primitive confined to any particular family. The main phyla probably developed along independent lines, thus leaving us with many wholly unrelated modern families in which characters which are generally accepted as primitive still exist. A broad survey of the anatomy of the modern Angiosperms gives a picture of certain groups of families such as those included in the order Malvales, which possess so many characters in common that it is reasonable to assume that the constituent families are phylogenetically connected in the sense of having had a common ancestor. Other families, such as the Pittosporaceae and Protaceae, possess no anatomical characters sufficient to indicate the nature of their nearest relatives beyond refute. They may, in fact, possess no modern relatives, and did we but know their past geological record it may well be that such families have followed an independent evolutionary development from a pre-angiospermic stock. In my opinion, the isolated position of families should be fully recognized in systems of classification wherever this seems desirable, rather than attempt to relate them phylogenetically to other existing families with which they may, in fact, never have had any connection. As new geological discoveries are made and our knowledge of present-day Angiosperms increases, it seems probable that the structure of vascular systems, and in particular of the secondary xylem, is most likely to afford evidence of the lines along which phylogenetic and evolutionary development may have taken place ; but the anatomist, palaeobotanist and taxonomist must always co-operate in interpreting results and drawing conclusions if any real advance is to be made. Even now I believe our knowledge of anatomy has advanced so far that a reinvestigation of early Angiosperms whose anatomical structure has been preserved, but whose affinities have never been well established, might well prove fruitful. The true affinities of some of them could not be fully established when they were first discovered because the anatomy of the modern Dicotyledons was then not adequately known (cf. Stopes, M. C., ‘ Petrifications of the earliest European Angiosperms ’, Phil. Trans. Roy. Soc. ser. B, CCIII, pp. 75–100 ; 1912).

ON THE TAXONOMIC VALUE OF THE ANATOMICAL STRUCTURE OF THE VEGETATIVE ORGANS OF THE DICOTYLEDONS.

2. THE TAXONOMIC VALUE OF WOOD ANATOMY.

By L. Chalk, M.A., D.Phil., Imperial Forestry Institute, Oxford.

Classifications of wood anatomy, like those of general systematic botany, can be divided into two categories, artificial or special and natural or general, using the terms ‘ special ’ and ‘ general ’ in the sense recently suggested by Turrill (1942), a ‘ general classification being based on correlation between the largest possible number of characters and a special classification being based on correlation between a limited number of deliberately abstracted characters ’. Special classifications are being discussed in another paper, and I propose to limit myself to the general classification of wood, or rather to the use of wood anatomy in general taxonomic classifications, as a means of increasing the number of characters available for correlation.

It is possible to set about making groups of woods in the same way that the taxonomist makes groups of plants, and so to build up a completely independent classification of woods, but in practice it is obviously foolish to ignore all the taxonomic evidence, particularly as this is based on a much wider range of material and of characters. What the systematic wood anatomist tends to do instead, therefore, is to try to fit his woods into the groups determined by the taxonomist, which is obviously quite a different problem. Instead of being primarily concerned with sorting out his units into whatever groups seem most satisfactory, the systematic wood anatomist is, much of the time, trying to find out which characters remain constant, and to define them in such a way as to allow for what one might call legitimate variation, such as that caused by difference in degree of specialization or differences in habit or habitat. For example, it is useful to combine the diffuse and metatracheal types of parenchyma under the term apotracheal, in order to emphasize the point that the difference between them is one of degree only, in that either type may occur in closely related genera or even in species of the same genus.

To use an analogy that I fear will be unfamiliar to many of you, the wood anatomist is, so to speak, able to cheat, by looking up the answer in a crib and working out his solution backwards—normally a dangerous procedure if the crib is not entirely reliable, and in this case it is not even certain that the crib is based on exactly the same text. However, let us assume to start with that the taxonomist has provided the right answer, in the sense that he has grouped together a number of genuinely related genera into a homogeneous family. One would expect that the woods would be similarly homogeneous and exhibit relatively few or minor differences. Actually the differences are often found to be numerous, and it is only when one is able to distinguish the significant resemblances from the insignificant differences, such as may be due to conditions of growth, that the group appears homogeneous. The Sapotaceae and Ebenaceae, or even the two combined into the Ebenales, form relatively homogeneous groups, though superficially the differences may be more striking than the resemblances; unless one can assume, for example, that the differences in the distribution of the parenchyma are merely less or more highly specialized variations of the same basic type, the essential unity of design may not be clear. In the large group of Leguminoseae there are certain combinations of characters that nearly always enable one to recognize a leguminous wood, but there is no single character that will do this, and even the combinations of characters must allow for considerable variation according to the degree of specialization in the particular species or genus.

It is mainly by studying such relatively homogeneous groups that it is possible to gain knowledge of the taxonomic significance of the various wood characters; but there is obviously some danger of becoming involved in a vicious circle. This may be expressed as follows: certain wood characters indicate relationship because they remain constant in taxonomically homogeneous groups, and certain taxonomic groups are homogeneous because certain wood characters remain constant.

Let us now turn to the possibility that the answer given in the crib is only partially correct, starting with the comparatively simple case of a small family that is homogeneous from the taxonomic point of view, except for one doubtful genus. Let us assume that this is really out of place owing to parallel development, or owing to reduction of the flower having limited the evidence as to where else to place the genus. Though parallel development certainly occurs in wood too, the chances are probably very much against this coinciding with that in the flower, and there is little reason to suppose that reduction in the flower will be accompanied by, say, equivalent changes in the water-conducting elements of the wood. There is, therefore, a high degree of probability that the genus will stand out clearly in its wood anatomy from the rest of the family and fit more readily into another family. The following are some examples :—In the Ochnaceae, *Lophira* ; in the Simarubaceae, *Castela* and *Holacantha*, which, however, resemble each other ; in the Theaceae, *Asteropeia* and *Tetramerista*, which differ both from each other and from the rest of the family. On the other hand, where a family exhibits a wide range of variation in wood anatomy, it may be difficult to produce adequate grounds for excluding any one genus. As examples I may cite *Goupia* in the Celastraceae and *Ctenolophon* in the Linaceae. The latter can be fitted into the Linaceae, but appears to be nearer to the Humiriaceae (Heimsch, 1942). Yet even in such cases wood anatomy may help by providing fresh evidence, which, though not conclusive in itself, may be significant when combined with other data. On the whole, therefore, it can be fairly claimed that wood anatomy does offer very considerable promise of aid in placing the difficult genus, and also in deciding whether some genera should become monotypic families.

Turning now to groups larger than the genus, one of the points that is most striking in wood anatomy is the uneven value of the sub-divisions of the family. In some families particular sub-divisions are clearly marked in the woods ; for example, in the Rosaceae the members of the Chrysobalanoideae are more clearly distinguished from the genera of the other sub-families than are many families from one another, while the Pomoideae, Prunoideae, etc., cannot be clearly separated from one another, though they are characterized by different tendencies. Not infrequently, however, the sub-divisions of a family bear no apparent relation to the wood anatomy. The latter may be so uniform that it suggests no obvious sub-divisions, or, at the other extreme, the woods may fall into definite groups, which, however, run counter to the systematic grouping. Examples of all these types may be found in the group of orders Tiliales, Sterculiales and Malvales, where it is, broadly speaking, easier to recognize a wood as belonging to the whole group of orders, if the Elaeocarpaceae be excluded, than to assign it to any one family.

At the level of the genus Chattaway has suggested, on the basis of the wood anatomy, the sinking of *Brachychiton* and *Eribroma* in *Sterculia* and the sub-division of the latter into two subgenera (Chattaway, 1937). In the Tiliaceae she found evidence supporting the separation of *Microcos* from *Grewia* (Chattaway, 1934). *Catostemma* appears out of place in the Bombacaceae, resembling rather *Cola* or some species of *Sterculia*. *Cistanthera* in the Tiliaceae is very suggestive of *Mansonia* in the Buettneriaceae, and so on. Among the tribes that are distinct may be mentioned the Sterculieae and the Elaeocarpeae, and the raising of both of these to the rank of family is fully backed by their wood anatomy. The Durioneae of the Bombacaceae may be cited as another tribe that is well defined. Others are less convincing.

The moral to be drawn from all this, I suggest, is that, with our existing knowledge, the most important rôle of wood anatomy is that of Bow Bells speaking the lines 'Turn again, Whittington'. It is just where the anatomical evidence conflicts with accepted taxonomic grouping that it is likely to be most valuable, and I may add that, in my experience, whenever such cases have arisen there has already proved to be some element of doubt about the taxonomy.

I do not wish to imply that the succeeding lines about being Lord Mayor of London have been permanently 'cut', in the sense that wood anatomy has no constructive suggestions to make. There are some highly specialized features, such as the oil and mucilage cells of the Lauraceae and Canellaceae, that are of obvious positive significance; but it may well be found that this type of feature helps where no help is needed. There is also an increasing volume of research in systematic wood anatomy that is steadily increasing the effectiveness of its positive contribution. The fact remains, however, that wood anatomy includes only part of the evidence, and is, therefore, less well fitted for constructing a general system of classification than for acting as a touchstone for the classifications produced by the taxonomic botanists. One obstacle to progress is the difficulty of bringing the doubts and problems of the systematist to the notice of the wood anatomist. In this connection it is well to remember that systematic wood anatomy is very dependent on adequate collections of woods and microscope sections, and that these collections have been built up mostly by forestry services and institutions in which interest and research tends, if not otherwise encouraged, towards special, rather than general classification, towards the practical problems of identifying particular timbers rather than to the general problems of taxonomy, and to the study of the mature secondary xylem of large trees rather than to the study of the primary or secondary xylem of herbaceous plants, shoots and young stems.

I have so far carefully avoided the subject of phylogeny, hoping thus to qualify as one of the angels, but in conclusion I must refer to one aspect of wood anatomy that may prove to be its greatest contribution to general taxonomy, namely, the significance of the length of the tracheary elements and of the cambial initial as a measure of specialization. Initiated by the investigation of Bailey and Tupper (1918), published in 1918, and elaborated by Frost (1931) in his studies of the vessel in the Angiosperms, this hypothesis has proved extremely fertile and has been widely used as a clue to variation in other elements and to the recognition of specialized and unspecialized forms. Bailey and Tupper's original investigation covered such a wide range of plants—from the Cycadales to the Angiosperms, and including fossil woods from the Cordaitales and Bennettitales—that it can be claimed, as Tippo (1930) has stated, that the conception of reduction in the length of the tracheary elements as an index of specialization has been formulated independently of any notion that this or that group of Gymnosperms has given rise to the Angiosperms or any preconceived ideas as to the degree of specialization of different groups of Angiosperms. Consequently it offers a possibility of escape from the vicious circle, recently referred to by Turrill, of a group being primitive or advanced because its members have primitive or advanced characters and vice versa. It also appers to offer reliable evidence as to the relative degree of specialization of different groups within the Angiosperms, and so may prove valuable as a check on series, genealogical trees and hypotheses as to the derivation of one group from another.

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ON THE TAXONOMIC VALUE OF THE ANATOMICAL STRUCTURE OF THE VEGETATIVE ORGANS OF THE DICOTYLEDONS.

3. THE RÔLE OF ANATOMY IN THE PRACTICAL IDENTIFICATION OF COMMERCIAL TIMBERS.

By B. J. RENDLE,

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IN identifying any biological material it is obviously essential to have a clear conception of the features which distinguish one species from another: that is to say, we must discriminate between characters which are relatively constant and those which are liable to vary under different environmental conditions. It so happens that the more obvious, gross anatomical features of wood are liable to show considerable variation under different conditions of growth. The constant, truly characteristic features often need a microscope for their examination. The process of preparing microscopic sections of wood is rather laborious and calls for a certain amount of apparatus. Much can be done by a trained observer under field conditions with an ordinary pocket lens and a hand specimen of timber, but for really accurate work laboratory facilities are essential. Even microscopic features show some variation within the limits of individual species, and the more variable of these are unreliable for the purpose of identification. Considerable experience is required to recognize the essential diagnostic features of a timber and to assess their value as family, generic or specific characters. In fact it is only in recent years, and after much intensive research, that the relative value of anatomical characters has been properly worked out. This has made it possible to develop a universal key for the identification of commercial timbers, using features of proved diagnostic value. Previously there were quite a number of good keys available, but these were confined to the timbers of a particular country or a single taxonomic group, and were thus of limited value for identifying timbers of unknown origin. It has to be remembered that in normal times the number of commercial timbers in regular use in this country runs into hundreds, and that they are drawn from all parts of the world.

Anyone whose job it is to identify specimens of timber almost daily naturally gets to know the common commercial species and the characteristics of well-defined families and genera, but there are occasions when he must have recourse to a key. It is, of course, unsatisfactory to depend on a key for the final determination of a specimen. Identifications should be confirmed, wherever possible, by reference to a good description or an authentic specimen. Many published descriptions are too sketchy to be of much value for identification. Others are overloaded with superfluous detail and often fail to specify the distinctive features of the wood. Much descriptive work has been spoiled because timbers have been studied as individual units, without regard to their affinities. It is much more satisfactory to make comparative studies or monographs of all the timbers in a natural group, and some excellent work of this kind has been done, but the difficulties of assembling the requisite material for such studies are obvious. Really good descriptions are rare, and in practice it is necessary to have access to an extensive collection of timber specimens and microscope slides. The collection should be extensive in two senses. Firstly, it should include all timbers of economic importance, and secondly, every timber—or as many as possible—should be represented by a number of specimens to cover the normal range of variation. The vegetative parts of a plant are subject to more variation than the sexual organs, and in the case of wood the difficulty of selecting a single typical specimen of reasonable proportions is increased by the large size of the average tree trunk. Thus the principle of referring to a type specimen cannot be applied to timber in quite the same way as it is to herbarium material.

It is not to be expected that the fine morphological differences which often separate closely allied species will always be reflected in the anatomical structure of their wood. Herbarium workers are well aware of the difficulties of determining a plant from imperfect material, and they will readily appreciate that a piece of wood represents a plant in a very imperfect condition indeed. Specific identification of timbers on purely anatomical grounds can sometimes be made when the number of species in a genus is quite small. But in the case of large genera with many species this is rarely possible without relying to some extent on circumstantial evidence.

In practice the determination of the species is not always necessary. It depends on how closely the commercial classification—or rather the commercial nomenclature—can be related to the botanical classification. Thus a commercial timber may be the product of a single botanical species, it may be a group of related species, or in certain cases it may be a particular grade or local form of a species; for instance, sapwood and heartwood may be graded as separate timbers, or timber from a particular district, such as Slavonian oak (the Austrian oak of former times) may be recognized as a distinct commercial variety by reason of its special qualities.

In northern Europe, owing to the comparative poverty of the tree flora, common timbers, such as ash, beech, walnut and pine, are each the product of a single Linnaean species. In the case of genera with more than one timber-producing species the specific differences may to some extent be reflected in the timber, as in the elms, or they may be insignificant, as in birch or oak.

It is interesting to compare this state of affairs with the position in North America, where the same genera are represented by comparatively large numbers of species. There, in the course of generations of practical experience, it has been found expedient, from the timber-user's point of view, to segregate the half-dozen principal species of ash into two groups. Similarly the deciduous oaks, numbering more than 30 species of economic importance, furnish only two main types of timber, corresponding to the sub-genera *Leucobalanus* and *Erythrobalanus*. The same sort of grouping has taken place in the case of the American hickories, birches, maples, pines and others.

It is found that the timbers of these sub-generic groups are generally distinguished by constant and well-defined differences of anatomical structure. Broadly speaking, then, it comes to this: where two or more related species have practically the same structure they may be regarded as being identical so far as their timbers are concerned.

Reverting to the practical identification of timbers, it is often the case that several closely related species of a large and widely distributed genus are identical so far as their wood structure is concerned. The field may be narrowed down and a specific name assigned to the timber with a high degree of probability by having regard to circumstantial evidence. If the specimen in question is known to be a commercial timber we are fairly safe in confining ourselves to those species which are known to produce timber of economic importance and likely to be used in this country in commercial quantities. At the same time we have to be on our guard against the possibility of exotic specimen trees from parks and gardens finding their way to local sawmills and thence to timber yards, particularly at the present time, when home-grown timber of every kind is being pressed into service.

As regards the possibility of using family characteristics in the identification of timbers, some well-defined families or groups of related families show combinations of anatomical features which are remarkably distinctive, so that their timbers can be recognized almost at a glance. On the other hand, families often appear extremely heterogeneous so far as the structure of their timbers is concerned, sometimes, no doubt, because the family contains only a small proportion of commercial timbers and these do not fairly represent the family as a whole. There is the further consideration that for purposes of identification we are on the look-out for points of difference rather than points of resemblance, and the tendency is to make use of well-marked, distinctive features regardless of their significance in indicating natural affinities. Features of this sort may be developed independently in widely separated families, or again they may be present in some members of a family and absent from others. In practice, therefore, the classification of timbers for the purpose of identification does tend to cut across the accepted botanical system, though probably no more than any other artificial method of classification.

ON THE TAXONOMIC VALUE OF THE ANATOMICAL STRUCTURE OF THE VEGETATIVE ORGANS OF THE DICOTYLEDONS.

4. FOSSIL PLANTS.

By T. M. Harris.

The fossil botanist, having queer and, maybe, unsatisfactory material, has often been forced to resort to methods without which the ordinary systematist has been able to get along. In particular, dealing as he does with isolated leaves, or often fragments only of leaves, he turns to such features as he can recognize, after chemical treatment, in the arrangement and shape of their epidermal cells. I shall deal with a few examples from this side, partly because I am more familiar with them than other aspects of fossil plant anatomy and partly because I think they should fit in with the matters under discussion for recent plants.

Fine anatomy is used for two purposes in the taxonomy of fossil plants :—

(*a*) To recognize species or to discriminate between them ;
(*b*) To recognize larger groups, genera, families, orders.

(*a*) The recognition of a species is the commonest problem of fossil botany. You may recall a famous instance where the Pteridosperm *Lyginodendron* was pieced together as a result of the recognition of peculiar glandular hairs on all the organs ; but there is a less ambitious problem facing the investigator every day. He has, say, 100 specimens picked out of a large collection of leaves of roughly similar appearance : are they all the same species ? He makes up his mind that they probably are, because their range of variation seems continuous, but he will not feel very sure about it. He now prepares their cuticles (which reflect the epidermal structure). If they are all similar his confidence that the specimens are all of the same species is enormously increased. It is a fact that there is a great range of types of epidermal structure, and leaves of similar aspect often have widely different cuticles. Closely related species sometimes have similar cuticles it is true, but unrelated species which happen to have similar gross form have as a rule entirely different cuticles. Cuticle structure and gross form seem to be independent variables, and where they both point to the same conclusion you feel much greater confidence than when you have one alone.

I will not discuss why the fossil botanist should need to recognize species, but I would merely say that nearly all progress, both in the morphological side and on the geological side, involves the recognition of specific identity or difference.

(*b*) The value of the recognition of larger groups is hardly fundamental for progress, but is an enormous convenience. To take an example among the fossil Gymnosperms. There are a lot of Cycad-like leaves which were formerly called 'fossil Cycads'. Then, when it became obvious that some had Bennettitalian flowers, they were called 'fossil Cycadophytes', a vaguer term, and the position of the majority of species was undetermined. Then H. H. Thomas and Bancroft recognized two contrasted types of cuticle in the group. In one (shared, indeed, by living Cycads, Conifers and Ginkgos) the epidermal cells round the stomata are not as a rule placed directly opposite the guard-cells, and it is clear that they have no immediately common origin in development. In the other group there are always two subsidiary cells exactly opposite the guard-cells, the whole apparatus being formed by the subdivision of a single cell. This is found in all the Bennettitales so far investigated, and it allows you to divide the 'fossil Cycads' into two groups—Bennettitales and the rest; the rest being largely or entirely true Cycads.

On the other hand, there is no constant difference between the stomata of the phyla, Cycads—Conifers—Ginkgos—Pteridosperms, but, of course, the gross form of the leaf is different enough as a rule. If you are working on leaf material, you must rely on characters of gross form to decide whether it is a fossil Conifer or a fossil Ginkgo, and if its cuticle shows features commoner in the one group than the other it gives some support, but only a little. The value of the cuticle to distinguish genera is much less clear. In some groups I believe it goes far to do this; in the living Conifers, for example, you could make a very fair identification of a genus if given 1 sq. mm. of a leaf; you would not always be right, but most of the errors would be to mistake it for an allied genus.

In the Bennettitales, on the other hand, I believe you cannot do this at all.

For example, the two genera *Ptilophyllum* and *Otozamites*, which look different enough as a rule, have no difference in cuticle such as I would care to define; and the genus *Pterophyllum* shows among its numerous species the whole range of cuticle structure that is found in the Bennettitalean class. Perhaps, however, *Pterophyllum* is itself a composite genus, but in any case it is true to say that the cuticle is not so helpful in distinguishing genera here as in the Conifers.

I would put forward as a generalization that in the taxonomy of fossil plants the study of form as visible to the naked eye, and of the minute features say 1 sq. mm. of the cuticle, are of about equal value. Each has its limitations, and sometimes one, sometimes the other is the more valuable. In fossil botany you can seldom go to work with a clear plan, but you have to be an opportunist, accepting with gratitude each helpful thing that turns up.

Referring to Dr. Chalk's paper, Prof. Harris asked that wood anatomists should publish their keys, together with a clear indication of the points which should be looked for in describing secondary dicotyledon wood. Fossil dicotyledon wood is often abundant and well preserved, but fossil botanists avoid it because they feel that the time they might spend in describing it would be wasted.

ON THE TAXONOMIC VALUE OF THE ANATOMICAL STRUCTURE OF THE VEGETATIVE ORGANS OF THE DICOTYLEDONS.

5. THE ANATOMY OF THE PETIOLE AND ITS TAXONOMIC VALUE.

By Dr. C. Leighton Hare.

It is encouraging to find in most systematic circles a genuine desire for collaboration with workers in other fields and a real appreciation of the part which these can play in the solution of taxonomic problems. In the quest for a natural system of classification the taxonomist, the geneticist, the cytologist and the anatomist each has a distinctive contribution to make, for evidence of affinity can be gleaned in all these separate but cognate fields of study.

It has now become abundantly clear that the internal structure, no less than the external form of the plant, is subject to the influence of heredity, so that endomorphic as well as exomorphic characters call for full consideration in all attempts to determine real relationships. Our knowledge of the comparative anatomy of flowering plants is, however, far from being complete, nor is it likely ever to form a basis for far-reaching changes in classification. It is, indeed, almost certain that morphological characters, especially those derived from the flower, will always remain the most important, as they are the most convenient criteria for classifying the Angiosperms.

No anatomist would suggest the adoption of a completely new system of classification based on internal structure; his true rôle is a less spectacular, but doubtless a more useful one, namely, to effect improvements to the existing system, through readjustments and modifications, where these appear to be justified on anatomical grounds. Inevitably his material is arranged in accordance with one or other of the current taxonomic systems, all of which show broad agreement in the delimitation of families and genera, though they differ widely in the interpretation and arrangement of major categories. Examining his material within this general framework, the anatomist learns to respect it, for he soon finds that anatomical data most frequently confirm the groupings based on floral characters. But it is not always so; sometimes they tend to different conclusions. A single instance will serve to illustrate a conflict of this kind. Within the Caprifoliaceae the majority of genera agree closely in most anatomical features and appear to form a natural association, but the anatomy of *Sambucus* ill accords with its present inclusion within this family, for it differs from the rest in characters which there are good grounds for regarding as of major taxonomic value. Some unusual features in the morphology of *Sambucus* lend support to this conclusion, for the genus is exceptional in the extrorse dehiscence of its anthers, as well as in its compound leaves and interpetiolar stipules.

Again, it sometimes happens that the taxonomist is uncertain of the true affinities of a particular family or genus; floral characters alone may not suffice to determine its position with confidence; when this is so, anatomical examination will sometimes reveal an unsuspected relationship. In such ways as these both groups of workers can give each other reciprocal aid, each employing his own special technique and independent data to check the other's deductions. There is here, I believe, a wide field for fruitful collaboration and a strong case for maintaining a closer liaison than has hitherto been attempted.

If the anatomist is to pull his full weight in such a partnership he must, however, make sure that he exploits to the full the material at his disposal, and this he has not always done. Much of the early work in systematic anatomy was based on an examination of the young stem and leaf alone, the root received but little attention, except in plants where it was known or believed to have some therapeutic value. This is unfortunate, though it has to be recognized that root material is sometimes difficult to obtain, so that even now our knowledge of the anatomy of the root lags far behind that of the stem. Again, it is only in comparatively recent years that the secondary wood has been extensively studied; but of all the parts of the plant it would be safe to assert that the petiole has suffered the worst neglect. This is the more surprising since this part of the plant is almost always easy to obtain, it can be quickly prepared for examination, while it has a much higher taxonomic value than is commonly realized. I am anxious not to give the impression here that the petiole has in the past been entirely ignored. A few valuable studies have indeed appeared, but most have suffered from being too limited in scope, and since the structure of this organ is remarkably varied, it is essential to examine a large amount of material if the conclusions arrived at are to have any general validity. The narrow scope of most studies of the petiole is, I believe, the main reason why its taxonomic value has hitherto been insufficiently appreciated.

Before dealing with this aspect of the subject I must refer briefly to the general structure of the petiole. What are, in fact, its distinctive features? It may be said at once that many of its tissues closely resemble those of the stem of the same species and are arranged in a similar manner; moreover, when special structures, such as secretory canals, latex tubes, crystals, etc., are present in the stem they commonly occur also in the petiole, and in the same relative positions. The shape of the cross-section and the form of the vascular system are, however, quite different in the two organs, in the stem they exhibit radial symmetry, in the petiole bi-lateral. Again, the conducting tissue of the stem, except in certain climbing plants, rarely departs from a simple hollow cylinder in herbaceous species, and a solid or nearly solid one in those of woody habit, whereas in the petiole it takes an astonishing variety of forms. What is the real meaning and significance of these peculiarities? Have they arisen in response to some immediate biological need, or are they at least in part fortuitous and independent of function? Now it has been widely held that a fortuitous character has a higher value as an index of relationship than one which is clearly related to some definite function, so that this is a question of particular interest and one which cannot be ignored in assessing the phylogenetic value of petiole anatomy. It can be answered with more confidence by considering for a moment what is in fact the function of the petiole. It will, I think, be generally conceded that it is two-fold. It serves in the first place as the channel through which the water utilized in transpiration passes to the lamina. This aspect of petiole structure was studied by Dr. Salisbury some years ago, and he found evidence of a correlation between the total cross-sectional area of the water-conducting tracts and the transpiring capacity of the leaf, and a further one connecting this area with the force required to shear the petiole at the plane of section. While this goes far to account for the total amount of conducting tissue in a given petiole, it does not explain its peculiar arrangement, and this is the petiole's most characteristic as well as its most useful diagnostic feature. I suggest that the clue to this feature is to be found in the bending effect of the leaf. At any cross-section of the petiole this will depend jointly on the weight of the lamina and the distance of its centre of gravity from that section. Considered from this point of view the petiole is, in fact, strictly comparable to a beam fixed at one end and supporting a weight at the other; hence it is subject to quite definite mechanical laws. In designing such a member there can be no doubt about the form its cross-section should take: it must be one that provides the maximum resistance to bending in a vertical plane, and at once we have the typical U-shaped, I-shaped or hollow cylindrical sections always employed in structures of this kind. Now it is highly significant that the main vascular system of the petiole, with its associated fibrous elements, can nearly always be reduced to a few relatively simple forms, each of which corresponds closely to one or other of the sections to which I have just referred (the apparent complexity of many petioles is due to the presence of additional minor vascular strands supplementing those of the main system).

In order to illustrate this principle, I have arranged in fig. 1 a number of typical cross-sections of actual petioles, grouped in vertical columns in three main series corresponding to the three types of vascular system referred to above. The U-shaped and cylindrical types are much the commonest; the I-shaped is less frequent in modern plants, though in *Populus* there is a close approach to a dissected form of it. It is interesting to recall, however, that among the fossil ferns of the genus *Zygopteris* this form of vascular system was typically developed. A single example is given, but the different species together form a remarkable and well-known series.

We must, I think, conclude that the characteristic vascular anatomy of the petiole has arisen primarily in response to mechanical needs—it takes precisely the forms best suited to sustain the continuous vertical flexure resulting from the weight of the leaf, as well as the intermittent lateral stresses due to wind action. If this is so, then its distinctive features should be regarded as mainly adaptive and functional, and for this reason they have, I believe, little phylogenetic significance. This is borne out by the fact that closely similar petioles are often met with in quite unrelated families—the common problem of support has been solved in a similar way in a whole series of different lines of descent.

One must beware, however, of over-simplifying a biological problem,

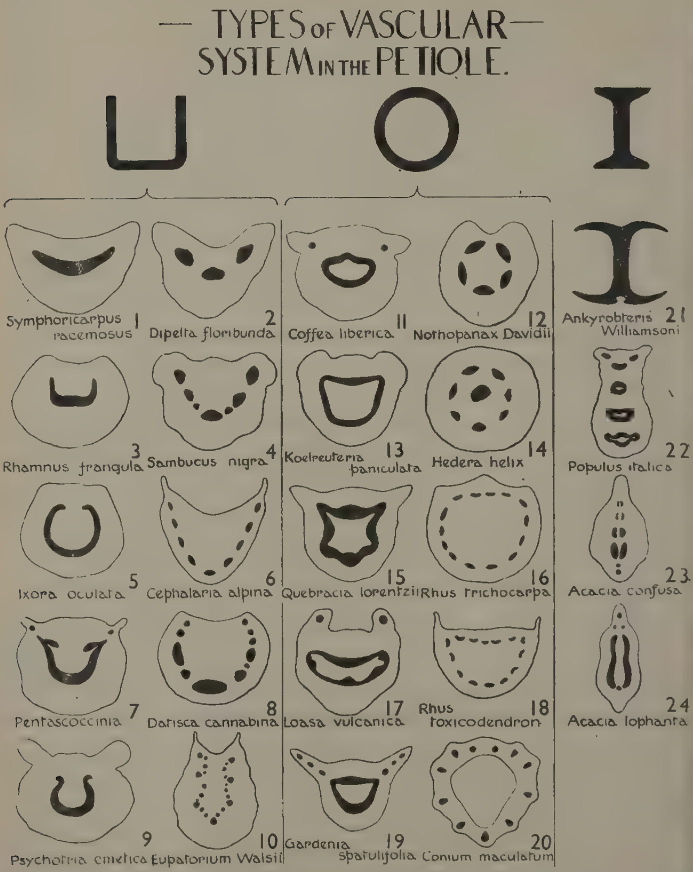
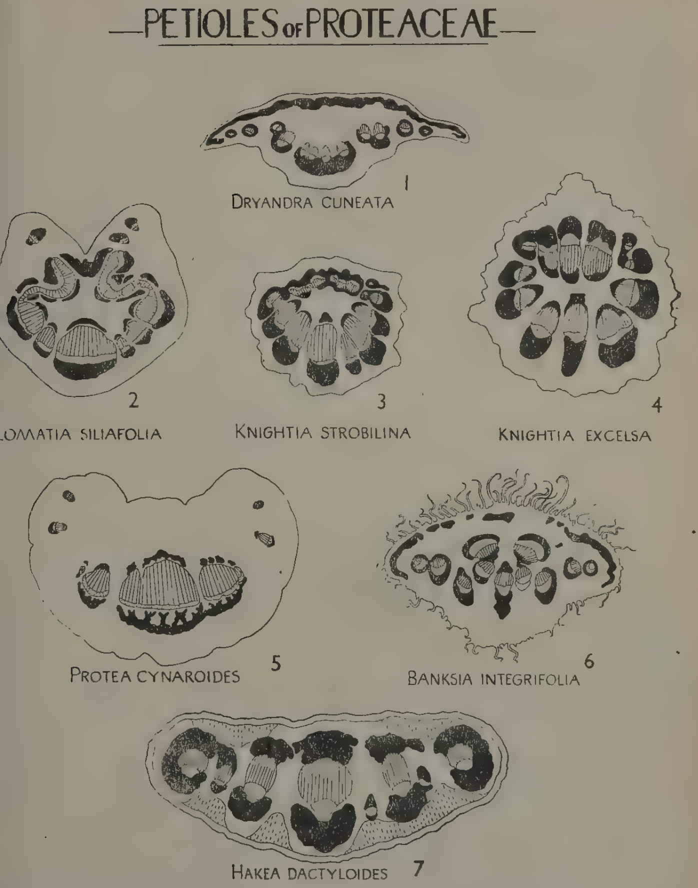


Fig. 1.—Diagrammatic cross-sections of a series of petioles to illustrate the three main types of vascular system. (Drawn to different scales; vascular tissues shown in black.) 1, *Symphoricarpus racemosus*; 2, *Dipelta floribunda*; 3, *Rhamnus Frangula*; 4, *Sambucus nigra*; 5, *Ixora oculata*; 6, *Cephalaria alpina*; 7, *Pentas coccinea*; 8, *Datisca cannabina*; 9, *Psychotria emetica*; 10, *Eupatorium Wallsii*; 11, *Coffea liberica*; 12, *Nothopanax Davidii*; 13, *Koelreuteria paniculata*; 14, *Hedera Helix*; 15, *Quebrachia Lorentzii*; 16, *Rhus trichocarpa*; 17, *Loasa vulcanica*; 18, *Rhus toxicodendron*; 19, *Gardenia spatulifolia*; 20, *Conium maculatum*; 21, *Ankyropteris Williamsoni*; 22, *Populus italica*; 23, *Acacia confusa*; 24, *Acacia lophanta*.



IG. 2.—Petioles of six genera of Proteaceae, to show the marked generic differences between them. (Xylem hatched, phloem dotted, sclerenchyma in black.) 1, *Dryandra cuneata* ; 2, *Lomatia siliafolia* ; 3, *Knightia strobilina* ; 4, *Knightia excelsa* ; 5, *Protea cynaroides* ; 6, *Banksia integrifolia* ; 7, *Hakea dactyloides*.

d it would be unwise to press the mechanical analogy too far. Other ctors must have brought about the wide diversity of detail in petioles different plants. Within prescribed limits they show, in fact, immense ariety, and it is this which gives them their real taxonomic value, for we have here a fresh set of characters which might be used to supplemen those commonly employed in classification. Before he uses them, th systematist will want to know how constant they are. Now experienc shows that they are, in fact, highly constant, for the different forms hav become stabilized. Characters derived from the petiole can therefor be used with confidence, but their value for purposes of classificatio varies widely at different taxonomic levels.

Sometimes, as for example in the Ericaceae and Rhamnaceae, th petiole shows little diversity throughout the family ; more commonl there is a range of different forms, each characteristic of a particula genus. A striking example of this is found in the Proteaceae. In thi family the anatomy of the young stem is markedly uniform, so tha on this basis it would be difficult, if not impossible, to distinguish th separate genera, yet the petioles are so distinct that they provide simple and ready means of recognition (see fig. 2). It is evident tha in this family the petiole has a high diagnostic value at the generi level. Or we may take the Umbelliferae : here is a family in whic generic determination is notoriously difficult in the absence of ripe frui yet the petioles are so distinct for each genus that of themselves the provide the means for a rapid provisional diagnosis. Within a give genus the vascular system shows great constancy of form, but mino variations will sometimes aid in the determination of species (compar for example the petioles of *Knightia excelsa* and *Knightia strobilina* i fig. 2).

I have already mentioned that petioles of closely similar type are no infrequently met with in quite unrelated families ; their comparativ value is then limited to the confines of a known family. In some gener however, the vascular structure of the petiole appears to be uniqu though without examining every genus of flowering plants it is of cour impossible to be certain of this. It may be of interest to close wit two examples of such unique petioles that have come under my noti recently. In the genus *Saxifraga* the petiole always shows three isolate vascular bundles arranged in a slightly curved arc ; each of them is centri not collateral, in structure and each is surrounded by its own separa endodermis. I do not know of any other petiole that could be confuse with this. Dr. Sprague has drawn my attention to the fact that th two genera *Bergenia* and *Peltiphyllum*, until recently included in *Saxifrag* have lately been separated from it ; it is therefore of interest to no that in both of them the petiole is quite unlike the true saxifrage typ If the latter proves to be quite constant for the genus *Saxifraga* evidently provides a simple way of separating the closely allied gener Again, a very curious example is found in the genus *Populus* (see fig. 1 Here the petiole is always more or less strongly flattened in a vertic plane near the distal end, where it is provided with a series of separa vascular bundles arranged one above the other (already referred to together I-shaped in general outline). This peculiarity immediate explains the familiar 'trembling' of poplar leaves in the slightest breez for it is obvious that the upper part of the petiole provides scarcely an lateral or torsional rigidity. It is difficult to imagine any useful purpo served by this continual movement of the leaf, and if, in fact, it has iological significance, then clearly we have here an instance of a truly ortuitous anatomical character.

It would be easy to give further illustrations of the taxonomic value f the anatomy of the petiole, but I have, perhaps, said enough to show hat if used with discretion and understanding it can be of real service the systematic botanist.

Both Dr. Sprague and Dr. Turrill have recently emphasized the nportance in taxonomic work of securing the maximum correlation of haracters, and the principle applies with equal force in systematic natomy, where we cannot afford to neglect any part of the plant that an yield us additional useful characters. This, I believe, the petiole an do, and in closing I venture to suggest that the practice of examining , already in force in some laboratories, might with real advantage be ore extensively adopted.

N THE TAXONOMIC VALUE OF THE ANATOMICAL STRUCTURE OF THE VEGETATIVE ORGANS OF THE DICOTYLEDONS.

6. THE RÔLE OF ANATOMY IN CONTROLLING THE ADULTERATION OF CRUDE DRUGS.

By T. E. WALLIS, D.Sc. (Lond.), F.I.C.

ANY crude drugs derived from the vegetable kingdom when entire, even in a somewhat broken condition, are quite easily named because ey show clearly recognized gross characters associated with the drugs question. Since, however, such drugs are often much shrunken, umpled or otherwise changed by drying and preparation, it is often a atter of much difficulty to distinguish them from closely allied subances or from skilfully selected adulterants. Nevertheless, there are r most drugs and adulterants certain structures, frequently microopical, by which they may be definitely recognized. Plant anatomy therefore, an essential part of the equipment of the pharmacognosist. me examples will show the manner of application.

Leaves of dandelion have been marketed as henbane leaves because, ien dried and shrivelled, they have a superficial resemblance to henbane, gely because both leaves have a wide, flat midrib. Similarly, leaves *Ailanthus*, the tree of heaven, are substituted for or mixed with lladonna (Allen and Deane, 1914), spearmint (Markwell and Cross, 35), or senna (Mitlacher, 1911). In practice, the general appearance certain pieces of leaf in the sample arouse suspicion, and these are oarated for further examination, and it is frequently anatomical tails which provide the definite evidence required. Thus, by cutting nsverse sections of the midribs of the leaves named above, differences found which clearly demonstrate the admixture of a foreign leaf d frequently, also, give a definite clue to its identity. Further conmation is obtained from the characters of the epidermal cells, the omata, the trichomes, the presence or absence of crystals of calcium alate, and their form and location when present. It might seem that possible adulterants are almost infinite in number, and consequently ficult to name; one may remember, however, that an adulterant must be cheap, easily obtained and resemble superficially the genuine article, so that only a limited range of material is available. In general, all likely adulterants have been used in the past and their characters have been recorded, and a little careful thought, aided by imagination, will usually provide a clue which can be confirmed by investigation.

In relation to a leaf like senna, a rather different problem arises. Some samples of Alexandrian senna are difficult to distinguish from Indian senna, and, since the Alexandrian leaf commands a higher price, this difficulty has sometimes resulted in prolonged litigation. One particular anatomical method may be applied, being the only reliable character at present available. This is to determine the vein-islet number (Levin, 1929), which for Alexandrian senna is 25 to 30 and for Indian 19 to 23. The result obtained by this method can now be confirmed by determining the stomatal index, the value of which as a differentiating character has been recently established (Rowson, 1943). Another difficult example is to detect leaves of *Scopolia carniolica* or of *Solanum nigrum* in admixture with belladonna. The only reliable method is to determine the palisade ratio (Wallis and Forsdyke, 1938), which is 6 to 10 for belladonna, 3 to 5 for *Scopolia* and 2 to 4 for *Solanum*. The character of the trichomes present in leaves is also a very useful anatomical feature.

Portuguese or Spanish digitalis, from *Digitalis Thapsi*, is closely similar to *Digitalis purpurea*, but is easily detected (Dewar, 1933) by its trichomes, which are all glandular, usually uniseriate, with a unicellular spherical glandular head. Scarcity of cascara bark has led to its replacement with the bark of *Alnus glutinosa*, the black alder. Transverse sections of these barks show that cascara has no pericyclic sclerenchyma and that in black alder there is a well-defined band of sclereids in the pericycle; black alder also has no phloem fibres, which are present in abundance in cascara.

Rhizomes of dog-grass, *Cynodon dactylon*, have frequently been substituted for those of *Agropyron repens*, two rhizomes which are superficially very similar. That something is wrong is revealed by observing a reaction for starch with the iodine test, and precise information is obtained from the transverse section. *Agropyron* (Small, 1919) has two rings of sclerenchyma, one hypodermal and the other pericyclic; it also shows an absence of starch; *Cynodon* contains starch in the stelar parenchyma and has only one ring of sclerenchyma, which is in the pericycle.

Marsh-mallow (*Althaea*) root offered as belladonna root may be identified by its characteristic cell contents, certain cells containing mucilage which is absent from belladonna; other cells contain cluster crystals of calcium oxalate, whereas belladonna has microsphenoidal sandy crystals in certain cells. *Althaea* also is pentarch and belladonna diarch.

For the control of powdered drugs of vegetable origin, the most important instrument is provided by botanical anatomy, which gives fundamental information as to identity, and in its more advanced application also affords means of determining the proportion of adulterant present or the proportions of the constituents of mixtures. When examining a powder the first aim is to refer the material to a morphological group;

hat is, to decide whether a leaf or seed or bark or rhizome or other plant nember is present. This is accomplished by noting how the cellular lements are grouped together in the particles present, and also by ıoting the presence or absence of particular structures. The next peration is to establish the precise origin of the plant members identified, nd this is deduced from the details of the cells and cell-contents bserved.

A powdered wood, for example, is recognized by the presence of lements all of which are lignified and consist of vessels, fibres and arenchyma, while many of the particles show vessels and fibres crossed y plates of parenchyma from the medullary rays. For final identificaion one would rely upon such details as the thickness of the walls of he fibres, the type of pitting of the vessels, etc., the appearance of the nedullary rays in tangential section, the type of calcium oxalate and ther cell-contents.

The absence of certain anatomical elements is often quite as helpful s the presence of others. For example, if the powder is a bark, such as innamon, all xylem elements and all epidermal and palisade tissues re absent, as also are aleurone grains. A study of the cork cells, fibres, clereids, calcium oxalate and starch will usually lead to identification. The adulteration of a powdered bark by another similar bark may, owever, involve much exact work. The presence of cassia bark as n adulterant of cinnamon may be detected by the presence of much ork and by measurement of the starch grains and fibres, both of which re larger in cassia bark. If one is asked, as is usually the case, to say ow much adulterant is present, it is necessary to add still further recision to the anatomical details by determining the area of phloem bres per gram. Cinnamon contains 90 sq. cm. of fibres per gram, vhereas for cassia the area is only 12·5 (Saber, 1940). Using these gures one can easily calculate the percentage of cassia in a mixture vhen one has found the area of fibre actually present in the sample.

A powdered rhizome or root usually shows large vessels, much arenchyma, cork cells and frequently much starch, with a general bsence of chlorenchyma, palisade and aleurone grains. Ginger rhizome, or example, is recognized by its abundant scitaminaceous starch, its arge unlignified vessels, its numerous fibres, of which only the middle amella is lignified, and narrow elongated brown pigment cells accomanying the vessels. Exhausted ginger is often used as an adulterant or commodities such an gentian and colocynth, and can be determined y counting the number of ginger-starch grains present in a milligram f the material and making use of the fact that ginger contains 286,000 tarch grains per milligram (Wallis, 1943). These measurements of rea and counts of starch grains are all determined by using the fundanental fact that lycopodium of commerce consists of 94,000 spores per nilligram (Wallis, 1919). The lycopodium is mixed in definite proortion with the sample under examination and the ratio between the umber of spores and the number of starch grains or the area of fibres, etc., s determined ; then, by a simple calculation, the number of spores ounted gives the weight of the amount of the sample in which the starch rains have been counted or the area of fibres measured.

The type of anatomy used for the control of drugs is, therefore, definitely morphological, and includes a precise knowledge of the proportions of certain structures which are present in particular drugs. The anatomical features are always used in association with other important characters, such as taste, colour, odour, solubility and chemical tests for constituents, when making an identification of a drug or of the constituents of a mixture of drugs.

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ON THE TAXONOMIC VALUE OF THE ANATOMICAL STRUCTURE OF THE VEGETATIVE ORGANS OF THE DICOTYLEDONS.

7. A REVIEW.

By T. A. SPRAGUE, D.Sc.

THOSE who have heard the previous speakers must agree that the practical value of anatomy in identifying plants is indisputable, especially where the material is incomplete. As has been shown, anatomical examination is essential in naming crude vegetable drugs, fibres and timbers. In fossil plants—to mention a single category of characters—the value of cuticle structure in identifying isolated leaves has been demonstrated. Where a herbarium specimen is too incomplete to identify even the family from the external characters, the anatomy sometimes yields the necessary clues. Anatomical characters often suggest or confirm the true relationships of aberrant genera, as I can testify from personal experience (Sprague and Boodle in Kew Bull., 1909, p. 309; Sprague and Sandwith in Hook. Ic. Pl., XXXII, 1932, t. 3172; Sprague and Metcalfe in Kew Bull., 1937, p. 392).

The importance of anatomical characters in taxonomic classification has not always been realized. For this there are several reasons. Systematic plant anatomy is a comparatively young branch of science, and the data are scattered and still far from complete, as is shown by the urgent need for a revised and greatly augmented edition of Solereder. In how many species is the anatomical structure as well known as the external characters? What proportion of angiospermous genera has been investigated anatomically? It has been said that the utmost caution is necessary in separating species on anatomical grounds, but this need for caution has not always been appreciated by anatomists, and a certain amount of prejudice has, perhaps, been created by the proposal of new species solely on anatomical grounds—species which the taxonomist is unable to distinguish by means of external characters.

Then it must be admitted that the training of the average taxonomist does not enable him to assess the relative taxonomic values of particular anatomical characters. This is not surprising, since even the anatomist has difficulty in discovering those anatomical features least capable of modification by environment, and so of greatest taxonomic significance.

It may be useful to state certain conclusions reached by taxonomists as to the relative taxonomic values of external characters, as these conclusions seem equally applicable to anatomical characters.

(1) In taxonomy one must be an opportunist, accepting with gratitude any helpful character that may turn up [wording adapted from Prof. Harris's contribution].

(2) *Single* characters, if they are rare, may be useful indicators of *possible* relationship, but a *combination* of numerous characters of diverse nature or origin points to *probable* relationship. The same combination of relatively few characters may occur in two unrelated groups, but the greater the number of associated characters and the greater their diversity the higher is the probability that the occurrence of such a combination in two or more groups is due to common ancestry. A parallel is afforded by a legal conviction obtained by multiplication of circumstantial evidence.

(3) Differences of number, dimensions and degree are obviously of less taxonomic value than differences of kind.

(4) 'Fortuitous' characters ('such as have no relation to the environment nor to any biological function') are more valuable than 'biological' ones ('such as are in direct relation to some vital function or advantage'). The only explanation of the occurrence of a fortuitous character seems to lie in inheritance, whereas the same biological character may have originated independently under similar conditions in many different lines of descent.

(5) It is often stated that characters, to be of taxonomic value, must be constant, but in families and groups of higher rank the sporadic incidence of a relatively rare character may be a valuable indicator of relationship (Sprague in Huxley, 'The New Systematics', pp. 445, 452; 1940).

(6) The value of a particular character may vary from group to group: a character which is constant in certain groups may be variable in others.

A scientific taxonomist cannot afford to neglect any available character —whether external, anatomical, cytological, chemical, ecological or physiological (Sprague in Journ. Bot., LXIII, 1925, p. 10). There are several reasons, however, for the predominant position assigned to external characters. (1) As a rule they are more easily observable; (2) there is a very great number and range of them; (3) they include many independent variables: the causes and course of floral and vegetative evolution, for example, are extremely diverse; (4) external characters can be used for defining taxonomic groups of all ranks.

In species and groups of lower rank, the taxonomist gets most help from the cytologist and geneticist, whereas anatomical characters assume greater importance in the definition and diagnosis of genera and families. The number of constant external characters steadily diminishes from the species through the genus to the family and order, and the taxonomic incidence of such constant characters as remain becomes even wider and wider. At the species level the chief problem is to detect the constant differences between one species and another. Having got the species, natural sections and genera are discovered by placing together those species which show maximum agreement of their numerous constant characters. At the family level the problem is quite different. The families themselves are mostly well known and natural. The difficulty is to arrange them naturally in orders and higher groups. Inspection of descriptions of families of Angiosperms shows that most of their external characters have a very wide taxonomic incidence. Most of the floral characters correspond to *stages in the evolution of the flower*—stages which there is every reason to suppose have been reached independently in many lines of descent. Examples of such characters are epigyny, gamopetaly, zygomorphy, haplostemony, meiostemony, and the uniovulate condition of the ovary. Hence the classification of families according to the measure of agreement in their extant descriptions (which consist mainly of floral characters) may result in groups of more or less unrelated families which happen to have reached the same stage of floral evolution. The subclass Metachlamydeae (Gamopetalae), for example, is probably polyphyletic, and has recently (Pulle, 'Compendium van de Terminologie, Nomenclatuur en Systematiek der Zaadplanten', 1938) been divided into five groups attached to four separate series of Archichlamydeae (Polypetalae and Apetalae).

One of the principal problems of taxonomy is, accordingly, to discover a more satisfactory grouping of the families of Angiosperms. Here anatomical evidence is essential. On the whole, our present classification of Angiosperms, from species to families inclusive, seems to be approximately natural, but the same cannot be said of many of the orders and higher groups. Judging from external characters, such orders as Centrospermae, Rhoeadales, Malvales, Myrtales (in the sense of Bentham and Hooker), Ericales, Primulales and Tubiflorae seem to be natural; but many orders are clearly artificial, for example the Geraniales and Sapindales in the Engler system, which are separated on a single character, the positions of raphe and micropyle in relation to the placenta.

Dr. Metcalfe has urged that where there is reason for considering particular families as isolated groups we should recognize this in our systems of classification rather than attempt to group them with other existing families with which they may never have had any connection. To carry out this suggestion consistently would, I am afraid, disrupt any of our present systems. I suggest that we might maintain, side by side, two separate systems of classification, one for purely practical purposes, the other serving as a basis for future research (Sprague in Huxley, 'The New Systematics', p. 436; 1940). The practical system would include all the families and be used for catalogues, enumerations and the arrangement of material. The research system would include only such groups as appear to be natural after careful scrutiny of all available characters. Further groups would be added from time to time as the evidence justified their inclusion. The system would long remain very incomplete, but it would have the supreme merit of being based on thorough examination of available facts instead of representing merely individual opinions. When the main phyla of Angiosperms have been established on a firm basis, it may be profitable to indulge in speculations as to their origin. Hopes of radical improvement in their classification rest on organized collaboration of anatomists and taxonomists over a series of years. All great taxonomic institutions should have not only taxonomists and anatomists, but cytologists and geneticists as well, working together on a common scheme of research.

PROCEEDINGS OF THE GENERAL MEETING

24 June 1943

(a meeting in celebration of the centenary of the
Rothamsted Experimental Station)

held jointly with The Zoological Society of London

Mr. A. D. Cotton, O.B.E., President,
in the Chair.

The Proceedings of the General Meeting held on Monday, 10 June 1943, having been circulated, were taken as read and confirmed.

Read for the second time a certificate of recommendation of the following candidate for Fellowship :—Sir Murdoch McLeod, Bt.

The President reported the death of Mr. J. Scott Thomson, Fellow of the Society.

The following communications on Botanical Investigations at Rothamsted were read and discussed :—

> (1) Sir John Russell : The development of Agricultural Science at Rothamsted. (2) Dr. W. E. Brenchley : Minor elements and plant growth. (3) Dr. H. G. Thornton : Effective and ineffective strains of the Nodule Bacteria of leguminous crops. (4) Mr. F. C. Bawden : The nature of plant viruses.

(The papers were discussed by Dr. Bernard S. Dyer, the President, Dr. C. R. Metcalfe, Mr. F. C. Minns, Mr. D. J. Scourfield, Miss R. F. Shove and Dr. J. K. Spearing ; Mr. Bawden and Dr. Brenchley replied to questions.)

The President thanked those who had contributed the papers to the present meeting.

The President expressed the congratulations of the Society on the centenary of Rothamsted Experimental Station, and especially to Sir John Russell, who was retiring after thirty-one years as Director. He also voiced the wishes of the Society for the future prosperity of Rothamsted.

BOTANICAL INVESTIGATIONS AT ROTHAMSTED.

1. THE DEVELOPMENT OF AGRICULTURAL SCIENCE AT ROTHAMSTED.

By Sir E. John Russell, D.Sc., F.R.S., Director, Rothamsted Experimental Station, Harpenden, Herts.

The Rothamsted experiments were started by John Bennett Lawes, a young squire who, in 1834, came into possession of an ancient manor which had long been held by his family. He was fond of chemistry, but had no systematic training; he set up a laboratory first in a bedroom, then in a barn, and a neighbour aroused his interest in the question then much under discussion: why are bones so ineffective in some places and yet so useful in others? Lawes realized that the plant nutrient in the bone was the phosphate; further, that it was insoluble, but that after treatment with sulphuric acid it would become soluble and therefore presumably more available. Experiments with growing plants showed it was so. Mineral deposits of calcium phosphate were then being discovered; this material in its natural state was ineffective, but after treatment with sulphuric acid it became a good fertilizer. Other experiments showed the fertilizer value of nitrogen compounds, especially of sodium nitrate and ammonium sulphate; also of potassium salts. 'Artificial fertilizers' were thus introduced into agricultural practice, and their use has spread so greatly that about 14 million tons per annum were consumed before the present war. Lawes realized that he could not himself cope with both factory and field experiments, and in June 1843 he secured the services of J. H. Gilbert; together they carried out the long series of what are known all over the world as the Rothamsted Experiments. As the years have gone by a vast number of problems have been studied relating to the effects of the different fertilizers on the soil and also on the habit of growth, composition, and value to the users of the various crops.

Agricultural science was long regarded simply as a branch of chemistry. The first botanical investigations arose out of the fertilizer experiments. Addition of plant foods to the mixed herbage of a grass field did not affect all species alike: some increased more than others, and the floral type of the herbage became changed. Thus nitrogenous fertilizers increased the growth of grasses much more than of leguminous plants, while addition of potassic fertilizer and of phosphate encouraged leguminous plants. Starting with an ancient meadow of fairly uniform herbage containing some 40 or more different kinds of plants, Lawes and Gilbert were able by variations in nutrition alone to produce some ten or more completely different herbages. This was the first important piece of ecological work done in this country, and the methods of botanical analysis then used, while tedious and laborious, are still among the best we have. Later on Dr. Brenchley developed certain other branches which she will herself describe.

The agricultural significance of the pioneering French microbiological investigations on nitrification was speedily realized at Rothamsted, and

Warington began in 1879 the first soil microbiological studies in this country. They were so promising that when A. D. Hall succeeded to the directorship in 1902 one of his first activities was to invite H. B. Hutchinson to extend the work. This subject has since been developed very considerably by a staff of competent microbiologists under Dr. Thornton.

Meanwhile, agriculture was developing in the United States and in Canada, and their agricultural experiment stations soon found that water supply was far more frequent as the limiting factor in crop production than the supply of plant food in the soil. American soil science therefore became much more closely linked up with physics, especially the old branch which used to be called Properties of Matter, than with chemistry and microbiology. Hall was an excellent gardener and fully realized the importance of air and water supply to the roots of the plant and the consequent need for studying the soil as an environment rather than as simply a source of nutrients.

It was soon evident that the existing resources at the disposal of Rothamsted and other experimental stations were quite inadequate for a proper study of plant growth and crop production. The phenomena were too complex to be treated as subsidiaries of chemistry or botany; a whole scientific staff would be needed to deal with them. Mr. Lloyd George had set up the Development Fund in 1911: out of this provision was to be made for the prosecution on an adequate scale of research into agriculture and agricultural science. Hall left Rothamsted in 1912 to become its Adviser.

The writer was then appointed as Director and began the work of expansion, which has since continued. Departments were set up for chemistry, physics, microbiology and botany; later came plant pathology, entomology, insecticides, statistical science and biochemistry. Statistical science was introduced because it was realized that no two plants are quite alike, nor are any two areas of soil, even in the same field; in consequence it is not sufficient to use the experimental technique of the chemist or the physicist, who can safely assume that any two samples of the same substance are, or can be made, identical in properties. Under R. A. Fisher, and later F. Yates, new methods of experiment were devised suitable for variable biological material and capable of affording an estimate of the validity of the results obtained.

With this widening of scope has come the need for team work; for problems in agricultural science rarely fit neatly into the conventional divisions of science, and there is nearly always an overlap. Further, as the staff must be chosen pre-eminently for their scientific attainments, it may, and usually does, happen that they have no direct knowledge of agriculture. Some knowledge, however, has to be attained. These two requirements affect the choice of staff, but fortunately there has in the past been no difficulty in securing the services of men and women of the desired calibre, and if the Station is equally fortunate in the future its continued success will be assured.

BOTANICAL INVESTIGATIONS AT ROTHAMSTED.

2. MINOR ELEMENTS AND PLANT GROWTH.

By Dr. W. E. Brenchley.

Sir John Russell has outlined the genesis of the botanical department at Rothamsted in its relation to field work. When Sir Daniel Hall, at the beginning of this century, became Director a beginning was made on research into various fundamental problems, of which I will confine myself to one—the relation between various minor elements and plant growth.

The term 'minor element' needs some explanation. It is used to indicate those elements of which extremely small amounts are sufficient to influence the plant, either beneficially or harmfully. It in no sense indicates that these elements are minor in importance. In fact, biologists and agriculturists alike are becoming alive to the fact that these elements are of the greatest importance to the metabolism of the plant, and in this connection they are attracting attention much as vitamins have done in the economy of animal life. The complex chemical composition of soil renders it a very difficult medium on which to test the effect of minor elements on plants, as no real control can be exercised on the elements available to the roots. Such control is afforded by the water-culture method, and all the initial research has been carried out in this way. The primary difficulty was to obtain sufficient pure distilled water for large-scale experiments, as distillation from glass requires a great deal of attention for a relatively small supply. Tests with various metals showed that water distilled over polished silver gave results indistinguishable from glass-distilled water, and special stills were then manufactured and have since provided all the water needed.

Attention was first directed to a group of five minor elements already associated with plant growth in one way or another—copper, manganese, zinc, arsenic and boron. The range of concentrations tested was very wide, in an endeavour to pass from the toxic limits to the smaller amounts required for stimulation of growth, if it occurred. Toxicity was easily shown—copper and arsenic being about ten times more deadly in the stronger concentrations than any of the others, manganese and boron being required in relatively large amounts to be lethal. Stimulation was far more difficult to demonstrate, though it seemed evident that boric acid in great dilution was beneficial to peas, and similarly manganese appeared to exercise a general stimulation. The variation in the relative toxicity of various elements was well brought out in later work with copper, nickel and cobalt in connection with the possibility of increasing the cobalt content of herbage in areas where cattle suffer from 'coast disease', which is curable by small amounts of cobalt. Concentrations of copper sulphate which killed barley allowed fairly good growth with cobalt chloride. At border-line strength the response of the plants varied with the individuals, as was well shown with both cobalt and nickel.

One important feature in connection with toxicity is that in the presence of solid particles such as quartz, sand or soil the poisonous action is greatly reduced. Consequently, plants growing in soil may be able to make normal growth in the presence of an amount of a poisonous substance which would kill, or at least seriously damage, a similar plant in nutrient solution.

Over a period of fifteen years many attempts were made to grow beans in water cultures for various reasons, but always without success. It so happened that they were never tested in the boron experiments till 1921, when one of the entomologists, Dr. Davidson, wished to introduce various elements into the broad bean in connection with his work on the control of the bean aphis. Acting on my suggestion, he tried my five minor elements, and after a few weeks complained that all his plants were dead, except those receiving boron, which were trying to push through the muslin cages with which they were covered. Following up this clue, Dr. Warington proved conclusively that in the absence of a trace of boron growth is completely checked, owing to atrophy of the meristematic points and subsequent breakdown of the tissues. The growing points of stems and roots, the flower buds and also the meristematic tissues of the nodules on the roots are all affected. The latter point was proved in collaboration with Dr. Thornton. Further work showed that many other plants—various Leguminosae, melons, carrots, etc., also required boron, as little as one part boric acid in 2½ million parts nutrient solution being adequate. For a long time cereals failed to show deficiency, though this was demonstrated elsewhere, but eventually, with improved technique, spectrographic examination of the nutrient salts, and marked increase in the purity of analar salts, barley came into line. Evidently the boron requirement of barley is extremely low, and deficiency shows itself by failure to produce ears coupled with a great increase in the number of blind tillers. No other element can replace boron in plant metabolism—over fifty were tried without success. The function of boron is still unsolved, though there are indications that it is in some way connected with the calcium nutrition of the plant.

This apparently academic work has had valuable practical results, as many obscure plant diseases—hitherto classed vaguely as 'physiological'—are now known to be due to boron deficiency. Heart rot of sugar beet, raan of turnips, topsiekte of tobacco, and other ills of a couple of hundred crop plants are all curable by the addition of small quantities of borax to the ordinary fertilizer, and only about 12 to 20 lbs. per acre is required, as too much is unnecessary and may be harmful. Seed production of sugar beet may also be safeguarded, as plants showing slight symptoms of boron deficiency in their first year may be brought to healthy flower and fruit by a judicious application of boron before the second season.

In agricultural practice Chilean nitrate is the form in which nitrate of soda is usually applied as a fertilizer. In addition to nitrate this contains small quantities of a number of minor elements, and the importance of these has received much consideration. Boron and iodine are the two outstanding elements. Tests made over a wide range of crop plants showed that the boron supplied in Chilean nitrate is fully as effective as independent dressings. Even at a very early stage in growth the benefit is manifest. The value of iodine, however, is still unproven. It is very tempting to argue that as a trace of iodine is so essential to the well-being of animals, it must therefore be of similar benefit to plants. The elimination of all iodine from the environment is extremely difficult, but with the utmost care in this respect it has so far not been possible to obtain any indication that iodine is essential or even that it effects much improvement in growth.

Molybdenum is also present in Chilean nitrate, and claims have been made that it is essential for lettuces and tomatoes. In our first year of experiments sodium molybdate repeatedly improved the colour, size and weight of lettuces very considerably. Without any apparent change in technique, and with the same stocks of nutrient solution, it has not been possible to repeat the results, and investigations are still going on to ascertain the cause. With tomatoes grown in soil no increase of crop was obtained, but treated plants came into bearing about a week earlier than the rest. It remains to be seen whether this year's crop will bear this out. Too much molybdenum is very poisonous, stunting growth, turning the leaves golden-yellow and damaging the root system.

The more one works with minor elements, the more complex the problem becomes. The cumulative evidence seems to suggest that deficiency symptoms are not always entirely the result of an inadequate supply of some critical element, but may also be bound up with other factors at present not fully recognized. Future work will doubtless have to be concerned with these factors as well as with the direct influence of minor elements on plant growth.

3. EFFECTIVE AND INEFFECTIVE STRAINS OF THE NODULE BACTERIA OF LEGUMINOUS CROPS.

By H. G. Thornton, Soil Microbiology Department, Rothamsted Agricultural Station.

It is well known that the nodule-forming bacteria of the Leguminosae fall into groups that are in general specific to certain groups of host plant, species or genera. This paper deals with the further sub-division of these bacteria into strains within each host specific group. If a number of bacterial cultures be isolated from nodules on a single host species, these will be found to vary very much in the benefit that they confer on their host plant through nitrogen fixation. At one end of the range there are often to be found strains that are largely ineffective in this respect—scarcely increasing the nitrogen content of their host plant. Such ineffective strains are particularly noticeable amongst the nodule bacteria of clover and of peas and beans. We are now engaged in surveying the distribution of ineffective clover nodule bacteria in Great Britain and fnd these to be particularly abundant in the poor sheep pastures of hill districts in Wales, the north of England and Scotland. The study of these strains has the improvement of the clover growth in such pastures as its ultimate object.

Anatomical study of the nodules produced by ineffective strains shows that these contain a much smaller content of infected tissue than do effective nodules. In addition, the tissue disintegration and dissolution of the contained bacteria which eventually occur in all nodules takes place much earlier in those produced by ineffective strains. If these factors are taken into consideration, the amount of nitrogen fixed by a unit volume of bacterial tissue in a given time is the same for 'effective' and 'ineffective' strains. The latter are ineffective because they do not grow so well or last so long in the nodule as do the effective strains. It has been found that individual plants vary greatly in their response to the nodule bacteria. In a few plants, bacteria belonging to a normally ineffective strain can produce nodules of normal size and can benefit the plant. The converse can happen with a normally effective strain of the bacteria. There is some evidence that this variation in the response of the host legume is hereditary. If this is confirmed, it raises the hope that varieties of clover can be developed giving an effective response to infection even by a normally ineffective bacterial strain.

It may also be possible to mitigate the effects of a population of ineffective strains of nodule bacteria in the soil by supplying effective strains through seed 'inoculation'. Here, however, a difficulty arises owing to the acute competition that takes place in the root surroundings between different strains of nodule bacteria. Strains that compete successfully with others are those having a high initial multiplication rate in the soil. Strains have now been found that combine this high multiplication rate with effectiveness towards their host plant. Such strains can compete successfully with ineffective strains in the soil and should thus be useful for the purpose of 'inoculation'.

4. THE NATURE OF PLANT VIRUSES.

By F. C. Bawden.

From the many and varied problems that have been studied in the Plant Pathology Department at Rothamsted I have chosen to describe today the investigations that have been made into the precise nature of those mysterious entities known as viruses. Viruses can conveniently be defined as obligately parasitic pathogens, too small to be resolved by ordinary microscopical methods. Their scientific study dates back to 1892, when Iwanowski, a Russian botanist, showed that bacteriologically sterile filtrates of sap from tobacco plants suffering from mosaic were infectious. Thus tobacco mosaic was the first disease shown to be a virus disease, and most of the advances in our knowledge of viruses and virus diseases have first come from work on this disease.

During the next 40 years the number of recognized virus diseases increased steadily and considerable progress was made in symptomatology and in discovering the means whereby viruses are transmitted, but little or no information was gained about their nature. The matter was a subject of continual controversy, but in the absence of any evidence to the contrary, they were generally believed to be the smallest living organisms, essentially similar to bacteria, though with the unfortunate properties of being invisible and unable to grow in culture media. In the last seven years, however, considerable evidence has been accumulated, suggesting that many plant viruses differ fundamentally from any known organisms. From plants injected separately with several different viruses, specific proteins have been isolated, and all our available information indicates that these proteins are the viruses themselves. Similar proteins have not been isolated from any healthy plants, the purified protein preparations are infective at high dilutions, slight changes in the proteins lead to loss of infectivity and the properties of the protein isolated are those of the particular infecting virus. There is no absolute criterion of purity, but some of the purified virus preparations have been tested by many different methods and have shown no sign of heterogeneity. The preparations certainly contain no appreciable amounts of materials with particles larger than those of the proteins, so that if their infectivity is due to constituents other than the proteins, these constituents must be extremely small, and the evidence overwhelmingly favours the view that the proteins are themselves infective. The size of the protein particles varies with different viruses, but all so far examined have particles with weights equivalent to molecular weights in excess of a million. Thus, the scientific interest that used to centre around viruses because they were thought to be the smallest known organisms has largely disappeared, to be replaced by an interest in them as the largest known proteins.

Tobacco mosaic virus was the first to be isolated, and the claim was made that it was a crystalline globulin. This was shown to be wrong, and all workers are now agreed that it is a liquid crystalline nucleoprotein. Preparations of this virus show interesting and unusual physical properties, and their study by X-ray diffraction has revealed a regularity of structure previously unsuspected in solutions. Before 1936 it was tacitly assumed that all viruses were incompressible spheres and all calculations of their sizes were made on this basis. A cursory examination of the optical and physical properties of the purified preparations of tobacco mosaic virus was sufficient to show that this assumption was invalid and that the particles of this virus were greatly elongated. In ordinary light, solutions show a satin-like sheen ; if sufficiently concentrated they separate into two layers, the upper being more dilute and more opalescent than the lower. In polarized light the lower layer is birefringent, while the upper shows the phenomenon of anisotropy of flow. The solutions also have anomalous diffusion and viscosity. The greatly elongated particles found in purified preparations of tobacco mosaic virus may be, in part at least, an artefact produced during the course of purification. There is evidence from a number of different sources that the virus is produced in the plant as smaller particles, which can become attached to one another end to end to form long rods. The application of the electron microscope, by means of which direct measurements of the sizes of virus particles becomes possible for the first time, can be expected to settle this problem.

After tobacco mosaic virus, five others, affecting tomato, cucumber, potato and *Hyoscyamus* were isolated and found to have elongated particles, so that their solutions also showed similar optical phenomena.

When precipitated with acid or salts, however, most of these gave amorphous precipitates instead of the needle-like para-crystals of tobacco mosaic virus. The next to be isolated was tomato bushy stunt virus, and this was found to have strikingly different properties. The particles of this virus are spherical, so that the solutions show no unusual optical properties, and when precipitated in appropriate conditions it forms beautiful isotropic, dodecahedral crystals.

The virus disease we have studied most recently, tobacco necrosis, differs in many ways from the others. Most viruses spread readily from the point of entry throughout the infected plants to give a systemic infection, but in this disease symptoms are restricted to necrotic lesions on the inoculated leaves. We have found that there are several different viruses and virus strains that can cause the symptoms of tobacco necrosis, and, on purification, these behave differently. All of them appear to have approximately spherical particles, but when precipitated with salts the different viruses causing this disease separate in different forms. Some have given only amorphous precipitates, others have given crystals, one crystallizing as thin lozenge-shaped plates, a second as hexagonal prisms, and a third in a variety of forms, of which the commonest are dodecahedra, bipyramids and thin round laminae.

Elementary analyses.

Virus.	C.	H.	N.	P.	Ash.	Carbo-hydrate.
	%	%	%	%	%	%
Tobacco mosaic	50	7·3	16·5	0·5	2·0	2·5
Cucumber 3	51	7·4	15·6	0·57	1·5	2·4
Potato 'X'	49	7·4	16·4	0·45	2·2	2·7
Potato 'Y'	49	—	15·0	0·5	—	3·0
Bushy stunt	49	7·7	16·1	1·4	3·5	5·5
Tobacco necrosis	45	6·5	16·3	1·65	7·0	6·5

The viruses that we have purified have widely different properties and stabilities and are transmitted in different ways, yet all have been found to be chemically similar. Elementary analyses of six type viruses are given in the table. The figures for carbon, hydrogen and nitrogen are similar to those usually found for proteins, and the figures for the different viruses vary significantly only in their phosphorus and carbohydrate contents. All the viruses are nucleo-proteins, and sufficient nucleic acid can be isolated from each to account for so much of the phosphorus and carbohydrate contents that there is no need to suspect the presence of any other component containing them. The nucleic acid seems to be the same type in all the viruses, similar to, though probably not identical with, yeast nucleic acid. It differs from that known to occur in chromosomes in that it contains carbohydrate in the form of ribose instead of a desoxy-pentose.

X-ray analyses on these purified virus preparations have shown that the viruses are in a sense doubly crystalline. Not only do the particles arrange themselves in a regular manner to give visible crystals or liquid crystals, but the smaller units of which the particles are composed are also arranged with perfect regularity. Such analyses have also shown that the virus particles, even when in solution, do not contain any water. It is their chemical simplicity, the regular arrangement of their constituent units and their inability to take up water that most sharply separates viruses from even the simplest known organisms.

There has been almost as much controversy over the nature of the intracellular inclusions so characteristic of many virus diseases as over the nature of the viruses themselves. It cannot be said that this problem has yet been finally settled, but we can at least superficially reproduce the phenomenon *in vitro*. By mixing purified preparations of tobacco mosaic virus with different substances we can get either amorphous or birefringent precipitates, depending on the substance added and the proportion of virus in the mixture. While these precipitates differ in some ways from the amorphous and crystalline inclusion bodies found in tobacco plants suffering from mosaic, their formation at least suggests that the inclusions themselves may well be insoluble complexes formed by the virus combining with some constituent of the infected host plant.

Discussion.—

Dr. BERNARD DYER, as one of the now few surviving Fellows who had enjoyed the personal friendships of both Sir John Lawes and Sir Henry Gilbert, wished to join in expressing the thanks of all present to Sir John Russell for his delightful historical sketch of Rothamsted and its work, as well as to his colleague Dr. Brenchley for her illuminating résumé of her own work on the so-called ' minor elements ' in relation to plant life, and also to Dr. Thornton and Mr. Bawden for their very valuable contributions to the afternoon's symposium. He had known Rothamsted for some sixty-five years, and in his earlier days its soils had been placed at his disposal by Lawes and Gilbert for working out certain analytical whims of his own, as kindly recalled by Sir John Russell.

PROCEEDINGS OF THE GENERAL MEETING
8 July 1943

held jointly with the Zoological Society of London

Mr. A. D. COTTON, O.B.E., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 24 June 1943, having been circulated, were taken as read and confirmed.

The following were thanked for gifts to the Library since the last meeting :—Mr. Frederick Burke and the Botanical Gardens, Zürich.

The following Fellow signed the Obligation in the Book of the Charter and Bye-Laws and was admitted :—Lieut. F. D. Ommanney, R.N.V.R.

Read for the first time certificates of recommendation of the following candidates for ordinary Associateship :—Dr. John Gregory Hawkes and Dr. Chester Jones.

The following candidates were balloted for and elected Fellows:—Alec Lindsay Poole, Leon Raymond Hayward, William Homan Thorpe and Sir Murdoch McLeod, Bt.

The President reported the death of Prof. W. A. Setchell, Foreign Member of the Society.

The following communications were read and discussed:—

Dr. F. E. Zeuner. New reconstructions of the Mammoth and the Straight-tusked Elephant. (Discussed by Dr. A. T. Hopwood, Dr. Malcolm Smith, Mr. R. H. Burne and Dr. R. Melville; Dr. Zeuner replied.) [Printed below].

Mr. I. H. Burkill. The way in which the leaves of *Tamus communis* and Dioscoreas attain their light-fixed positions. (Discussed by the President.) [Printed on p. 252.].

The following communications were read in title:—

Mr. E. Nelmes. A key to the Australian species of *Carex* Linn. (Communicated by Dr. T. A. Sprague, F.L.S.) [Printed on p. 277.]

Mr. C. F. Symington, F.L.S. *Pseudosindora palustris* (Leguminosae–Amherstiae)—a new genus and species from Borneo. [Printed on p. 285.]

Dr. T. A. Sprague, F.L.S. A new species of *Rapanea* (Myrsinaceae) from Lord Howe Island. [Printed on p. 288.]

Mr. R. J. Harrison, A.L.S. Synopses of the British Fauna—No. 2. Key to the British Caprellidea. [Printed as a separate publication.]

The President then declared the Session of 1942–3 closed.

NEW RECONSTRUCTIONS OF THE MAMMOTH AND THE STRAIGHT-TUSKED ELEPHANT.

By F. E. Zeuner, D.Sc., F.Z.S., F.G.S.

Many attempts have been made to reconstruct the mammoth, for which excellent material is available in the shape of skeletal remains, of finds of bodies with flesh and hair in the frozen ground of northern Siberia, and of sketches made by Palaeolithic man. In comparison, the Straight-tusked Elephant has been much neglected, since skeletal remains are few, and there are not more than three Palaeolithic drawings which have been tentatively assigned to this species.

The models exhibited are the first of a series of Pleistocene mammals which was originally planned for dioramas. For this reason, the small scale of half an inch to the foot, or 1/24 of natural size, was adopted. They are the joint work of Miss I. Gedye, of the University of London Institute of Archaeology, and the present author, and have been acquired by the British Museum (Natural History), where they are exhibited in the Geological Department.

A.—*The two Recent Species of Elephant.*

Before describing the models it will not be out of place to recall that the two surviving species of elephants, *Loxodonta africanus* (Blum.) and *Elephas maximus* Linn., are only distantly related and exhibit peculiarities which distinguish them from one another as well as from the two fossil species under consideration.

The African Elephant is a decidedly high-legged creature with a pronouncedly flattened skull and with very large ears. The profile of its back is concave behind the shoulders, but becomes convex in front of the hind-quarters, the resulting prominence being, in normal standing attitude, as high as or higher than the head.

The Indian Elephant has a very different skull, with two large rounded prominences in the fronto-parietal region. Its ears are relatively small, and the profile of the back is straighter and sloping slightly towards the hind-quarters. On the whole, however, the level of the backbone remains much the same from the neck to the pelvis.

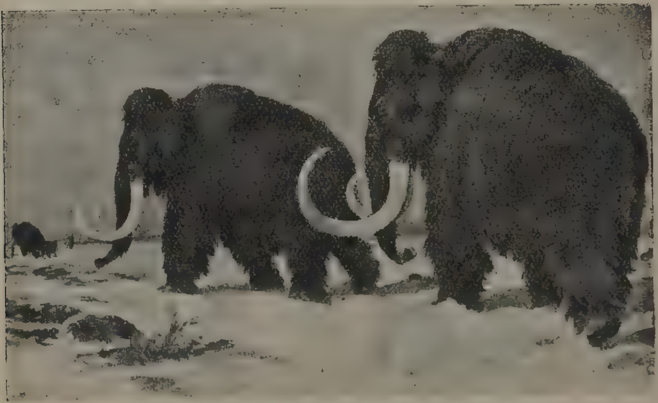


Fig. 1.—Reconstruction of the mammoth, by Roubal, under the direction of Abel. Painting in the Natural History Museum, Mainz.

B.—*The Mammoth.*

The mammoth (*Elephas primigenius* Blum.) is the best known of all Pleistocene mammals, and excellent reconstructions have been made in recent years. After several early attempts by various authors, which were not successful and are chiefly of historical interest (summary, Dietrich, 1912), O. Abel succeeded in producing a satisfactory reconstruction (Abel, 1912) which has become the prototype of most later representations. Among them, the paintings (fig. 1) and a model (scale about 1/15 natural size) executed by Roubal under Abel's direction (copy in the British Museum (Natural Hsitory)) are especially notable. Another group of reconstructions of the mammoth are those executed by Charles Knight under the direction of H. F. Osborn (Knight, 1935;

sborn, 1942). They consist of a series of vivid paintings showing the merican race of the mammoth in various positions in its natural environ- ent.

Curvature of the tusks.—The only important difference between the bel-Roubal and Knight-Osborn versions of the mammoth is in the rvature of the tusks. In the former, the tips of the tusks are turned utwards, in the latter inwards towards the trunk. Abel (1922) considers e outward curvature as a character of the European race of the ammoth. The skulls found in North America, the Beresowka mammoth nd some finds from Central Europe, such as the Borna mammoth, have sks bent inwards. Other specimens from Central Europe, however, ppear to exhibit the outward turn. Some specimens have aberrant sks: for instance, the skull of *Mammonteus primigenius compressus* sborn from Rochester, Indiana, U.S.A., whose tusks lie entirely in the lane of the alveoli (Osborn, 1942, fig. 1023) and are bent outwards. his specimen suggests that, whether outward curvature was a constant aracter of the European race of the mammoth or not, the feature as ch was within the range of variation of the species. For the new model, moderate inward curvature has been chosen, following the majority of he specimens known.

The chief external characters of the species were (for details, see Abel, 912, 1922; Osborn, 1942):—

Size.—The Siberian race was smaller than that of the Pleistocene f Europe, males attaining 3 m., females 2·5 m., of shoulder-height, mpared with 4·3 m. in the Mammoth from Steinheim, south-west ermany (Abel, 1922, p. 12. For comparison, Recent Indian Elephant, verage 2·8 m.: African Elephant, up to 3·5 m.).

Outline of body.—The skull was exceedingly high, and its outline raised uch above the neck. Numerous prehistoric drawings show a hump robably of fat) over and behind the shoulder, whence the profile of the ack dropped rapidly towards the hind-quarters. This outline is essenti- ly differt from that of either Recent elephant.

Thickness of body.—In cross-section, the bodies of recent elephants resent an almost circular outline, broken only by the slight crest of e backbone. In Roubal's model of *E. primigenius* the body is laterally mpressed, presumably so as to express the height of the hump. This fails to do, since the median line of the entire back is narrow and most crest-like, suggesting an unusually high backbone with curiously oping ribs. In the present reconstruction the body section of the ving species has been adopted. It is naturally further emphasized by he thick fur.

Some structural characters affecting external appearance.—The skull is t least as long as, if not longer than, the free portion of the trunk. This due to the great height of the cranium as well as to the length of the veoli. The latter are very close together, so that the rostrum is quite arrow. The face of the mammoth, therefore, was much longer than at of either recent species and curiously tapering, with the trunk in ont of rather than between the bases of the tusks. With its strongly volute tusks, the face of the mammoth must have been unlike that of odern elephants, especially in frontal view.

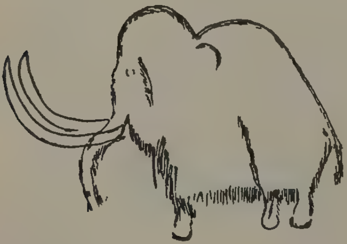
The feet, at least of the last Siberian survivors of the species, had four digits only, instead of the usual five found in other elephants.

The tip of the trunk, described by Flerov (1931) from a specimen preserved in ice, carried an upper and a lower pointed lip. This feature is also shown in a drawing from Les Combarelles in the Dordogne.

The bony tail was surprisingly short, though presumably continued by a good-sized tuft of hair.

The hair.—Remains found in Siberia and Alaska have proved that the mammoth had a coat of hair consisting of a woolly underfur which was very dense but only 2–3 cm. long, and of abundant, coarse, shaggy outer hair 30–50 cm. long, which covered the entire body and reached down to the toes.

The colour of the outer coat, as found, is a dark brownish-red, and this is the colour given to the mammoth in reconstructions. It is possible, however, that the red hue is the result of fossilization, since hair recovered from prehistoric graves also is frequently red. The mammoth, therefore, may after all have had black hair, much like that of young African elephants.* The suggestion that the reddish hue of mammoth hair is secondary is not new ; it was first made by Brandt more than seventy years ago. In the present reconstruction the conventional reddish-brown has been adopted, for lack of definite evidence to the contrary.



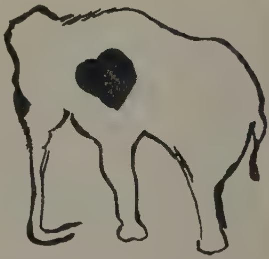


Fig. 2 (left).—*Elephas primigenius* Blum., Magdalenian drawing from the cave of Font-de-Gaume. After Breuil. Showing the hairy trunk.

Fig. 3 (right).—*Elephas antiquus* Falconer, prehistoric drawing from the Pindal Cave, northern Spain. After Breuil. With indication of a " mane ".

On the face the hair cover was dense and short. This is clearly shown by the prehistoric drawings, especially by those from Combarelles and Font-de-Gaume. The hair found on remnants of the trunk appears to have been as much as 30 cm. long, but I have been unable to find a statement regarding its density. The hairy trunk is shown in two cave drawings from Font-de-Gaume (fig. 2).

The cranium bore a huge wig. The hair of the body was shaggy and fell down over the flanks, to form the characteristic fringe under the belly, depicted in many of the cave-drawings. On the whole the new econstruction presents the mammoth as even more hairy than do the revious reconstructions, especially on the head, face and trunk.

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* Dr. A. T. Hopwood, however, informs me that the hair on *new-born* African Elephants often tends to be of a reddish hue.

C.—*The Straight-tusked Elephant.*

The Straight-tusked Elephant (*Elephas antiquus* Falconer) is known rom skeletal parts only. Three prehistoric drawings have been assigned o this species, one from the Pindal Cave, northern Spain (fig. 3), one rom the Sud Oranais, Algeria (both, Breuil, 1911), and one from Guébar-Rechim, Algeria (Pomel, 1895). The latter is regarded as *Elephas tlanticus* Pomel, a North African race of the Straight-tusked Elephant. The importance of these drawings was not fully realized until Osborn 1942) drew attention to them.

The mount of the elephant from Upnor, Kent, in the British Museum Natural History) (Andrews and Cooper, 1928) has much increased our nowledge of this species. The skull, unfortunately missing in the Upnor specimen, received special attention from Osborn (1942), who elied mainly on one of the Italian race, from Pignataro Interamna, which was complete when found. Two further skulls were discovered t Steinheim in Württemberg. The better preserved of these served or the reconstruction of the head, made by M. Böck under the direction f F. Berckhemer (1930).

Several drawings and a model were made in New York by Margret Flinsch Buba under the direction of H. F. Osborn (Osborn, 1942, p. 1216, ig. 1074 ; p. 1238, fig. 1092). The model is one-eighth natural size (copy n the British Museum (Natural History)). The body of these reconstructions is based on the Upnor Elephant. It includes all the features uggested by the Upnor skeleton, and the later drawing by Flinsch Buba 1937 ; in Osborn, 1942, fig. 1074) is as nearly perfect as such a econstruction can be. In the earlier drawing (1931 ; in Osborn, 1942, ig. 1092) and in the model the chest is somewhat too small for the size f the elephant, with the result that the fore legs appear rather too high.

The scarcity of fossil skulls and of prehistoric pictures raises the uestion whether the specimen from Pignataro can be regarded as epresentative of the whole species. Osborn did so regard it and used t in his reconstruction of the Upnor elephant (1942, fig. 1074). This vas justifiable, since, of the two Steinheim skulls, one lacks the upper ortion altogether, and in the other the fronto-parietal part of the ranium is almost entirely missing. Only part of the right side and the ack are preserved.

In the reconstruction by Berckhemer and Böck, the head is remarkably lat above. This flatness may be a character of the north German race f *E. antiquus*, or it is the result of the absence of the frontal and nasal ortions of the skull. The new reconstruction (fig. 4) follows the Italian kull, with some minor adaptations to the proportions of the northern pecimens known and to the Pindal cave-drawing, chiefly because the Italian skull agrees with the cave-drawings better than does the Steinheim kull.

The most important external features of *E. antiquus*, as shown in the econstruction, are the following :—

Size.—*Elephas antiquus* was larger than the average mammoth. The Upnor specimen had, in the flesh, a shoulder height of about 4 m.

Outline of body.—The absence of the long, shaggy hair of the mammoth makes *E. antiquus* appear more like an ordinary elephant. For the general outline of the body the Pindal drawing, together with the Upnor specimen, provides fairly reliable information. The drawing shows that the head was not low, but, in fact, was quite as high as the shoulder (a distinction from the African Elephant). The profile of the back slopes gently from the shoulder towards the hind-quarters, with a very slight depression over the loins. The pelvis-height was smaller than the shoulder-height, though much less so than in the mammoth. The legs appear higher than in the mammoth, because of the absence of long hair. The Pindal drawing shows *E. antiquus* almost as high-legged as *E. africanus.*

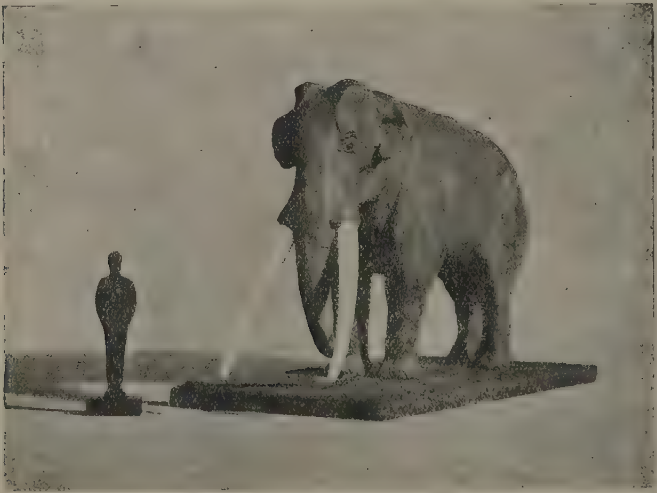

Fig. 4.—New model of *Elephas antiquus*. Photo, W. H. T. Tams.

The head.—The Pindal drawing gives an outline of the cranium which is borne out by the Pignataro skull, with a conspicuous, supra-temporal eminence. Osborn's reconstruction of the Pignataro skull accounts for this feature, which, apparently, is connected with the great development of the back of the cranium. In front view two such prominences are separated by a median depression.

The alveolar portion of the head is enormously developed. The alveoli are not only large, to hold the large, long tusks, but they stand wide apart, so that the width of the rostrum equals the maximum width of the cranium. The deep depression between the alveoles and the nasalia, found in the recent species, is entirely absent, so that, as in the mammoth, the trunk must have rested in front of the alveolar portion of the skull, presumably forming a distinct convex bulge.

The ear is regarded as small by Osborn. He relied on the two Algerian drawings, in which a line behind the head suggests something like the outline of the ear. If this interpretation is correct the ear would not have been larger than that of the Indian Elephant. The heart-shaped patch on the shoulder of the Pindal drawing, originally interpreted as the ear, is in a position which renders this interpretation unlikely (Abel, 1912).

Some structural characters.—The most extraordinary part of the skeleton of *E. antiquus* is its vertebral column (Cooper in Andrews, 1928). Its neural spines are at right angles to the longitudinal axis of the vertebra. In this character *E. antiquus* differs from all known elephants. It is difficult to say whether it influenced the external profile of the back, and in what way.

The hair.—The three cave-drawings assigned to *E. antiquus* suggest that this species was either bare-skinned, like the modern elephants, or covered with short or sparse hair which would not show in a sketch. I am inclined to favour the second alternative, chiefly because on the neck of the Pindal drawing is a series of short oblique lines which appear to indicate a kind of mane, or rough, long hair (fig. 3). Young Recent elephants also have a sparse coat of hair which is most conspicuous on the head and neck. It is conceivable, therefore, that *Elephas antiquus* was not entirely devoid of hair.

In concluding, I wish to emphasize that the models do not pretend to be works of art, nor even satisfactory representations of our knowledge of the external appearance of these species, although an attempt has been made to give expression to all those features which have been established or rendered reasonably probable. It is with great pleasure that I acknowledge the help received from Dr. A. T. Hopwood in the course of this work. He sacrificed much of his time in discussing the models repeatedly with me and in procuring publications difficult of access at the present time.

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THE WAY IN WHICH THE LEAVES OF TAMUS COMMUNIS AND DIOSCOREAS ATTAIN THEIR LIGHT-FIXED POSITION.

By I. H. Burkill.

The two photographs of fig. A (p. 253) were taken in the Royal Botanic Gardens, Kew, towards the end of July : they show vigorous plants of the indigenous *Tamus communis* Linn., Black Bryony, and the North American *Dioscorea glauca* Muhl. (*D. villosa* Linn., subsp. *D. glauca*) in side view. At Kew these plants have a position shaded against the western sun by a wall, but otherwise in the open, and they are given dead sticks for support, which arrangement makes them convenient for study, as there is no interference from leaves of supporting plants. It is to be noted in the photographs (i) that all the leaves of *Tamus*, save one, and all those of the *Dioscorea*, save three, point earthwards, but (ii) that the angle varies. There is nothing unusual in a plant which rises above the level of the field-layer of vegetation carrying its leaves with the apices downwards ; but there is considerable interest in the way in which the varying pose of the leaves of the Dioscoreaceae is attained.

The laminae of *Tamus* are in general of greater superficies than those of the shrubs which *Tamus* victimizes for support, and the long mobile petioles swing these laminae to positions of advantage in front of those of the victims. Lest they swing them also in front of the leaves of their own stem, internodes space them ; but when two *Tamus* stems intertwine, as they do often, some suffer. It is not easy to be concise and clear in describing this swinging, wherein all three dimensions, and time as well, are involved ; but I hope that by the aid of the figures the text is left without ambiguities.

Brenner illustrated a paper on *Tamus* (Verhandl. d. Naturforsch. Gesellsch. in Basel, XXIII, p. 127 ; 1912) by a pair of photographs of a single plant, the one from in front and the other from the side, and his illustrations, which reappeared in Kirchner, Loew and Schröter's 'Lebensgeschichte der Blütenpflanzen Mitteleuropas' (1/3, p. 709 ; 1930), are instructive and worth reference. In his text he calls attention to the varying angle and leads the reader to infer that it is determined by the need of obtaining light : so it is ; but he does not enter into any discussion of the way in which the pose is attained. My approach to the question was taxonomic, my chief reason for the investigation being that as Dioscoreaceae, which are certainly Monocotyledons with great specialization, exhibit in leaf striking morphological resemblances to Dicotyledons, a comparison of the behaviour of their leaves with the behaviour of the leaves of the most similar Dicotyledons, such as are found in the Leguminosae, Cucurbitaceae and Convolvulaceae, is a desirable object and likely to expose parallel evolutions of considerable interest. This paper is a contribution towards it ; and I believe that at the end the reader will admit that the Dioscoreaceae seems to possess so many less obvious differences that the more obvious resemblances to Dicotyledons are discountable.

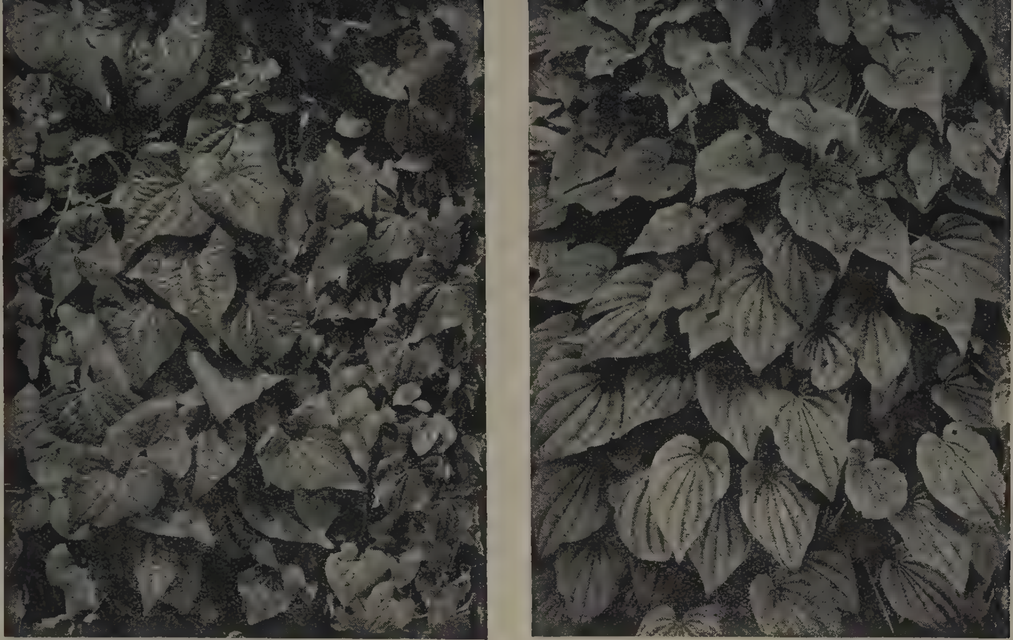


FIG. A.—On the left a side view of a vigorous plant or group of plants of common origin by division underground of *Tamus communis*, and on the right a similar view of an adjacent plant or group of plants of common origin of *Dioscorea glauca*, from photographs taken in the Royal Botanic Gardens, Kew, by Mr. Gerald Atkinson.

No Monocotyledons possessing pulvini offer closer similarities to the Dioscoreaceae than the Araceae, but the Araceae are not closely allied; they happen to have in common a climbing habit; and considerable need of adjustment of position.

Petiole movements during the unfolding of the leaves of Tamus.—Early in our British autumn the annual renewal of the shoots of *Tamus* commences. A bud in the axil of the basal scale-leaf of the dying stem of the year begins to grow and slowly, during winter, pushes its way upwards from the tuber towards the surface of the soil. The new stem is, so to speak, sessile, for there is no internode between its basal scale-leaf and the scale-leaf in the axil of which it arises; but the internodes above the basal scale elongate, and by their behaviour show that they have negative geotropism. The apex, endowed with rudimentary leaves, which are abundant, is bent into a crook with dia- to positive geotropism. When spring arrives this crook is thrust out of the soil and remains a character of the apex of the climbing stem (fig. B_2), although in very rapidly growing plants it may be somewhat straightened (fig. B_1). The stem, at a short distance below the apex, circumnutates in the direction of the clock, its impulse to circumnutate imposed over the negative geotropism, which, from characterizing the first internodes, advances up the stem. At the same time it develops a slight negative heliotropism by which it tends to lean away from strong light, an advantageous leaning, for it sends the stem towards any neighbouring

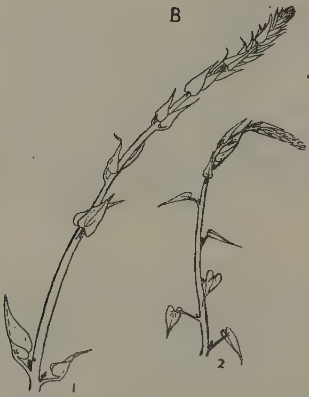


Fig. B.—1, the apical part of a vigorously growing shoot in May, at which time the leaves are expanding: note that their expanding is delayed so that the stem is unencumbered by them in its pushing upwards. 2, the apical part of a slightly less vigorous shoot, the shoot of a plant almost at flowering, small inflorescences appearing but not maturing.

ush and so towards a support ; or if the stem be at too great a distance rom such a bush, and on a bank, it sends it to lean against the vegetation f the bank (cf. Baranetzki in Mém. Acad. Imp. Sci. St. Petersburg, er. 7, no. 8, p. 23 ; 1883, where this negative heliotropism is recorded or *Dioscorea*). The early movements of the stem, its circumnutation or instance, carry the young leaves passively into whatever angle owards the pull of gravity and the incidence of light may be its own. These young leaves are held with the midrib parallel to the long axis f the stem and with the auricles embracing the stem, as fig. B shows.

Figure C takes up the history of the leaf at the time when the young eaves begin to move away from the stem. In it the youngest leaf is

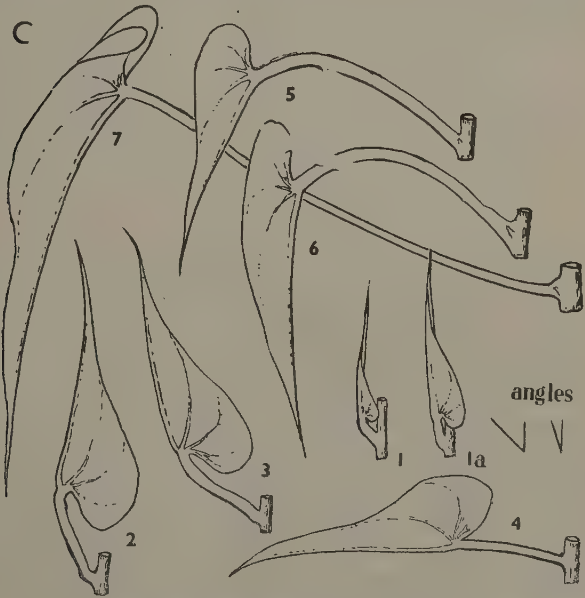


Fig. C.—Leaves of *Tamus* seen from the side ; all × 5, and numbered according to their age. Explanations in the text.

umbered 1 and the oldest 7. The youngest was 15 mm. long and is een with its petiole holding the lamina out at a little distance from the tem, an arrangement which permits a flowering panicle to have space or development in the axil. By the side of fig. C_1 is fig. C_{1a}, being a eaf from a stem too young to flower ; in it the petiole does not make he same accommodating angle, but holds the lamina closer to the stem, n which position, teleologically viewed, it is better placed, because it is less exposed to desiccation and is itself a protection to the stem. On the right of figs. C_1 and C_{1a} are drawn the angles made by the petioles respectively; they are,—for the flowering stem about 40°, and for the flowerless stem about 20°.

From the condition C_1 the petiole moves the lamina a little outwards merely by elongating (fig. C_2): but no sooner has this movement commenced than there is a local intensification of the rate of growth in the adaxial side of the petiole at base and apex, and this widens the angles at these places and therewith causes the midrib to be no longer parallel to the long axis of the stem (fig. C_3), with its angle to the pull of gravity altered. The leaf seems at this stage to be preparing to assert an independence, but not yet to have asserted it.

Condition C_3 is followed by a spreading of the increased rate of growth from base to apex along that side of the petiole where it has already been detected, namely, the adaxial side, whereby stage C_4 is brought about, and then C_5 and C_6. The petiole, by growing faster on the adaxial side than on the abaxial side, turns the lamina on the stem as a pivot, keeping the plane of the movement that of its own long axis, in which is the long axis of the stem; and so, though it may not have the same geotropism as the stem, or at least does not show it, it has not escaped from the control of the stem.

All movements up to this point must be regarded as ontogenetic: growth is not normal without them.

Subsequent petiolar movements, wherein the influence of an auxin made by the lamina takes effect.—From the condition C_6 the petiole returns to the straightness shown in C_7, passing through a condition resembling C_5 on the way; and that part of the petiole tends to remain straight which is between its first two angles, or immature pulvini; this part of the petiole may be conveniently called the shaft. In some petioles the movement by which it returns to straightness goes a little too far, rendering the side of the petiole which belongs to the face of the leaf slightly concave.

This return to straightness has a parallel in the behaviour of a climbing stem which will curve to enfold a support, but straighten if the support be removed, the straightening being a response to an internal urge to be straight, to which the rather unsatisfying name of autotropism has been given. When the shaft of the petiole of *Tamus* has attained straightness it is, so to speak, clamped at straightness, although still plastic to stimuli from without. But later the shaft indurates (fig. G_4, on p. 262).

If the lamina of a young leaf be removed during the changes which have been described, the petiole passes through them up to stage C_6 and then ceases to grow, ultimately dying down to the base. If, instead of cutting off the lamina, it be injured, the changes are carried through; and if we injure one side of the lamina, light is thrown on its procedure by the exhibition of a lateral interference in the behaviour of the petiole. Fig. D shows what happens. Putting together the experiments of removal and of lateral injury, there is no alternative conclusion than that the lamina produces an auxin and has commenced to pass it to the petiole, the growth of which it now controls. No attempt has been made to extract the auxin: but the two increased rates of growth, (i) that leading to the condition of curvature in fig. D, and (ii) that straightening the petiole, can happen so close together in time that they surely arise in the same way, i.e. from the arrival of the auxin, which enables the petiole to straighten by supplying the necessary stimulus, and this stimulus operates at least in causing straightening until the urge to remain straight fixes the straightness. With the supplying of the auxin, the leaf has shown an independence of the stem; but there is yet no proof of independent response to gravity and light.

The following comment, though speculative, is permissible. It is known that the travelling of auxins is impeded so much by cell-walls that it passes down tissues with elongated cells more quickly than across such tissues, and it is known that auxins may make of vascular tissue a path-way; comformably, arrival of an auxin in the petiole, regarded as sudden, may well be expected to take effect first where the vascular tissue would lead it, and that is where we find its first effects. But we are left with no way of explaining why the curvature of C_6 appears, only to be undone.

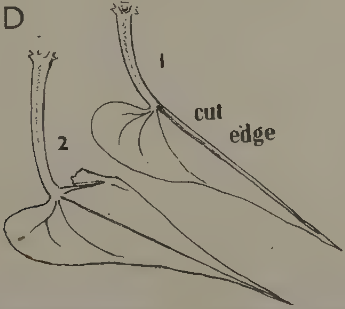


FIG. D.—The curves of petioles consequent on unilateral mutilation of young leaves, the one by cutting, the other by crushing, × 5. The mutilation was done at dusk and the drawings made on the following morning.

Petiolar movements in Dioscorea glauca.—The experiments made on *Tamus* have been repeated on *Dioscorea glauca*, which I grow in my garden from rhizomes obtained from Kew. The experiments, therefore, were done on the stock figured as A_2 (on p. 253). Some of the results are given in fig. E.

E_1, E_2 and E_3 are three ontogenetic stages in the normal growth of the young leaf: E_1 corresponds to C_3 of *Tamus* as regards the angle at which the lamina is held. At this stage the petiole of *D. glauca* is much less differentiated than the petiole of *Tamus*; its angles at base and apex are less defined and the base of the leaf is scarcely auriculate, whilst the many primary nerves are not spread out in a fan. E_2 leads to E_3, which corresponds with C_4 as regards curvature, but still exhibits the retardation of differentiation in the petiole and in the base of the lamina.

The series of movements in *D. glauca*, just described, end with the petiole rising towards the stem to a position suggested by fig. E_5. The corresponding rise in *Tamus* is somewhat less. The angle between petiole and stem thus brought about I would class as its ontogenetic angle. Its size in different species becomes a specific character to be expected of normal leaves.

The establishment of the angle is the last act of the growth on the abaxial side of the petiole by which the petiole is straightened. And just as the straightening of the shaft is abruptly stopped when straightness is attained, so does the narrowing of the angle seem to be stopped when the right degree has been reached. If it be admitted that the angle in C_1 is adjusted to allow an inflorescence to develop, it may be held that something outside the leaf, probably in the stem, determines the arrest of the narrowing of the angle.

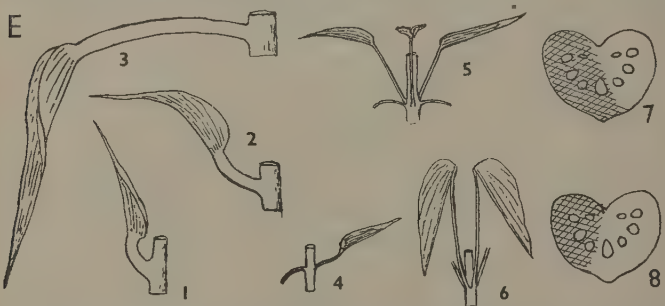


Fig. E.—*Dioscorea glauca.* 1, 2 and 3 the young leaf in three stages, × 5. 4, a pair of leaves of which the one was mutilated when in the stage of E_3, thereupon the petiole which had no lamina ceased to grow, and the control grew; also the petiole with no lamina failed to straighten itself as the control did. 5, a group of five leaves from which two laminae were removed at a stage slightly later than in E_4: the uninjured petioles grew and straightened, which the injured did not, and the former took a steeply ascending position. 6, two mutilated leaves of a group which, during a night, developed in the flank of the petiole on the uninjured side more growth than on the injured side; the increase of this growth not being exactly lateral, but slightly towards the abaxial side, a canting of the half-lamina results; 4, 5 and 6 × ½. 7 and 8, the petiole in section, × 5, showing the position of the vascular bundles. Explanations in the text.

At the time when this angle is being established, the angle also between petiole and lamina is being established.

Because *D. glauca* produces leaves in whorl-like groups, it has the convenience for experimental work of offering a control leaf by the side of a leaf taken for experiment, and of that I have made use (cf. figs. E_4, E_5 and E_6).

The arrest of growth of the petiole consequent on removal of the lamina is shown in figs. E_4 and E_5, and the arrest on the flank after lateral mutilation of the lamina in fig. E_6. It suffices to refer the reader to the legend under fig. E; but it is well to add here that the curvature of E_6 passed away later, passing upwards out of the petiole by what I regard as an autotropism.

A canting of the lamina invariably accompanies the onset of this curvature of the upper pulvinus, and also a relative decrease in the growth of the abaxial side of the pulvinus, which causes the lamina to droop its apex. All these three movements—the lateral curvature, the canting and the drooping—occur when the mutilation is greater than in fig. E_6 by the removal of the midrib or by a severing of the midrib towards the base of the lamina; but with this difference—that the drooping is increased. Figs. E_7 and E_8 represent the petiole in transverse section and show the vascular bundles in position; fig. E_7 stands for the lesser mutilation where the midrib is intact, fig. E_8 for the greater mutilation where it is severed or removed, the cross-hatched area including the bundles which have not suffered interference. On the assumption that auxin passes from the lamina by the bundles, its action is to be expected in the cross-hatched parts, which, growing faster than the rest, make the pulvinus to curve, along with which, the greater mutilation having cut the midrib, there is more retardation of growth on the abaxial side in E_8 than in E_7, and, therefore, more drooping of the apex. The canting, on the contrary, is not directly produced by these changes in growth, but is due to torsion accompanying the growth.

Let a young stem be taken which carries a group of leaves whose petioles have just acquired straightness in the shaft; train the stem into full light and fix it to an upright so that the group of leaves selected for experiment is free: then remove the stem beyond them and mutilate the laminae. This is the result of one such experiment wherein two leaves were mutilated on the first day and three on the second, the observations being made on the third:—

Declination from the horizontal	
of the control leaf, unmutilated	32°
of a leaf mutilated in the lesser degree on the second day of the experiment	40°
of a second leaf similarly mutilated at the same time	48°
of a leaf mutilated similarly on the first day of the experiment	60°
of a leaf mutilated in the greater degree on the second day	90°
of another similarly mutilated on the first day	95°

The lower pulvinus follows at a time-lag the lead of the upper, curving in the same direction. And so, when two adjacent leaves are mutilated alike but on contiguous sides, as in fig. E_6, the curvings of the lower pulvini as well as the upper cause the laminar ends of the petioles to approach each other. At the same time the torsion in the upper pulvini throws the apices of the laminae outwards, so that they are further from each other than the bases. But this condition passes away in the autotropic straightening of the upper pulvini; and, as this straightening proceeds, growth in the base of the lamina not only brings the apices into line with the petioles, but carries them further, so that, in a case of paired mutilations such as in E_6, after some days, the sooner the more active the growth, the laminae may cross each other. Of the effect of this growth in the base of the lamina, a few illustrations are given on page 268 forward: but my investigations in regard to it are incomplete, for I have not yet found how to control the amount of this readjustment.

A lamina slit from apex to base, but with no part of its tissues removed, gapes by growth at the junction of lamina and petiole.

The perception of the pull of gravity and of the incidence of light.—If a vine of either of these species be trained into a dark chamber and be fixed in it in an unnatural position, say with its apex downwards, the leaves thus rendered upside down right themselves by a slow movement. They are able to do this from an early age and keep the power while they retain the power of growth, though its strength wanes. Fig. F_1 indicates the movement towards righting executed in a night by petioles of *D. glauca* at the age when the return to straightness should be proceeding were they not inverted, i.e. at an age as that of fig. E_5. Fig. F_2 gives the reaction of slightly older petioles. This inversion experiment shows that the power to perceive and respond to the pull of gravity is in existence at the time when the passing of auxin from the lamina to the petiole is first demonstrable; and it is apparent that some part of the leaf is percipient, though the experiments do not suggest what part; for petiole and lamina had alike been inverted. In experiments to locate the percipient part the difficulty is met with of the petiole without a lamina being an organ which cannot grow; and for the present it is necessary to accept the position of knowing that the leaf as a whole is percipient without being sure how much of the whole is.

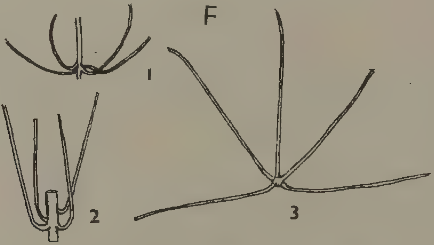


FIG. F.—1, the position taken during a night by the petioles of young leaves of *Dioscorea glauca* on an inverted stem. 2, that taken by slightly older petioles during the same period. 3, the position taken by petioles on a stem fixed horizontally; × ½. The laminae are not drawn, but were not removed. In F_3 the closely-set leaf-bases interfere with each other.

Fig. F_3 indicates that the power of response in the flank of the lower pulvinus is slow in taking effect.

Responsiveness to the incidence of light appears in the leaf about the same time as responsiveness to gravity; and the reaction to it increases in a way which ends in a complete obscuring of the reaction to gravity.

Inverted leaves on a vine of either species, freed from support and left pendent in the light, right themselves, responding in the first place both to gravity and to light; and finally they adjust themselves to the light. This they do deliberately; and manifestly it is to diffused light that they do so. Wiesner called plants which so adjust euphotometric. The group includes the Dioscoreaceae, along with most shade plants (cf. Biolog. Centralbl., XIX, p. 1; 1899). It may be remarked at once that the optimal intensity of light for *Tamus* is less than full sunlight; and it may be added that this is apparently why the rapidly growing shoot is inclined away from direct sunshine.

As of gravity, so of light we have no experimental proof that the petiole is percipient; but whether percipient or not, its behaviour shows that, as is common in plants, it is the servant of the lamina in reactions to light.

Tamus has sun- and shade-leaves, of which more presently.

Differentiation in the structure of the petiole and in the base of the lamina.—The loss, by ceasing to grow, of a power to respond to outside stimuli spreads in the shaft of the petiole of *Tamus* towards the ends with some rapidity, but, being arrested, leaves the ends still capable of growth as pulvini. For these in side view see fig. G, where G_1 shows the lower and G_2 the upper pulvinus of a well-grown leaf; G_3, G_4 and G_5 are sections through the lower pulvinus ($_3$), the shaft ($_4$) and the upper pulvinus ($_5$), at twice the magnification of figs. 1 and 2.

The pulvini at no time acquire any thick-walled tissue; but the shaft acquires such in a ring just outside its bundles (fig. G_4). All the bundles, as a rule, pass from end to end of the petiole. They are covered by more parenchyma in the pulvini than in the shaft.

The smaller bundles converge on the larger and are united to them where the lower pulvinus passes into the pediment; in the upper pulvinus, chiefly just under the hinge, cross-ties unite the bundles. I would stress this difference as important: it indicates a greater interference with elongating growth at the upper pulvinus than in the lower, for cross-ties appear where elongating growth is stopped and unions by approach where it is only modified.

In the 'Journal of Botany' (1939, p. 338) I illustrated the appearance of this locus of no elongation within the leaf-rudiment. It acquires the status of a diaphragm where growth-stimuli are filtered.

On the laminar side of this diaphragm a kind of hinge is brought into being at which four adjustments are made: (i) the angle between petiole and lamina is fixed; (ii) the primary nerves of the lamina are held apart like the ribs of an umbrella, so that they spread out a frame for the assimilating parenchyma; (iii) in a leaf in sunlight too intense for it, the weaker of these primary nerves, which are the outer, are pushed upwards so that the auricles present their surfaces obliquely to the light; and (iv) by differential growth on the side of the midrib canting of the lamina is produced. Minute corrugations may be seen on the back of the midrib as the result of adjustment of the angle (*rid.* in fig. G_2). The hinge and the upper pulvinus in combination constitute a locus in the leaf, where turgidity is more slowly converted into growth than elsewhere, and the delay suggests that although certainly euphotometric, *Tamus* inclines a little towards Wiesner's panphotometric group.

The upper pulvinus is obviously dorso-ventral, not only in structure, but in power to grow. It is most able to grow on the abaxial side and least able to grow on the adaxial side, its readiness to grow on the flanks being intermediate.

The lower pulvinus is somewhat less dorso-ventral, for though in internal anatomy it too is definitely dorso-ventral, it has but little difference on any side in readiness to grow. Is there some survival of ontogenetic origin in the stages by which the extreme dorso-ventrality of the lamina passes through the condition in the upper pulvinus of marked dorso-ventrality to the less marked dorso-ventrality of the lower pulvinus?

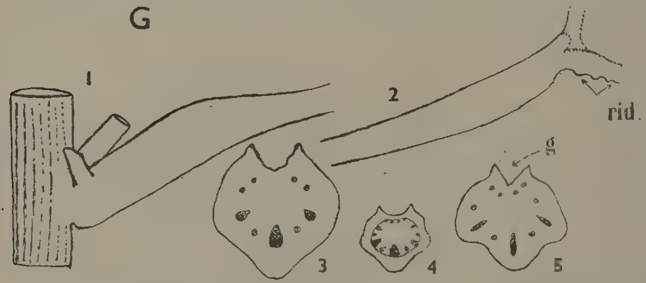


Fig. G.—The petiole of *Tamus*. 1, its lower end, and 2, its upper end in side view. In 2 the upper surface of the hinge is dotted and the ridges (*rid.*) are exaggerated, otherwise the magnification is 2½. 3, 4 and 5, sections through the lower pulvinus, the shaft and the upper pulvinus, × 5.

The more nearly columnar an organ is the more suited for movement; and the lower pulvinus is correspondingly a more general servant of the lamina than the upper. But neither pulvinus by simple growth can do all the adjusting which may be needed; the rest is contrived by torsion, which, though mostly in the lower pulvinus, extends, if required, to the shaft and to the upper pulvinus.

If the pulvini be slit medially in water, the two halves of the upper curve from each other in a very marked way, a demonstration of the presence of turgid cells in its deeper tissues. There is little of this gaping on slitting the lower pulvinus.

The extremes in leaf-form in Tamus.—Descriptions of leaves of *Tamus* in works on systematic botany never cover all the forms of leaf which the plant has. In a general way they indicate that which is commonest: outside it are four extremes. The first is the seedling leaf, a small reniform mucronate leaf on an upright petiole, more vernal than the leaves of the plant of its later years, and with a flat surface. Seedling life lasts for more than one year. The petiole in the first year arises immediately from a minute tuber: this first leaf is replaced by a similar leaf in the next year, but there is at this age a brief stem, on the top of which the leaf stands as if terminal; in the third year the stem is more evident, but is still topped by a leaf, though it is not necessarily the only functional leaf of the plant: there may be two. The lamina is now larger and acuminate. In the fourth year the stem liberates itself from arrest at a leaf and twines on finding a support.

The second form of leaf is the shade-leaf. It is produced by plants undergoing suppression from the overshadowing of taller vegetation, and under trees the stems commonly lie prone on the ground herbage. Of this form of leaf the petiole is apt to be more or less erect, and its upper pulvinus is straight: the surface of the lamina is flattish, with the assimilating tissue between the nerves scarcely at all bullate.

The third form of leaf belongs to a stem which has succeeded in climbing without reaching the top of the supporting vegetation, but, coating its side, it obtains lateral light. It too has a lamina which is flat, but the lamina and the petiole have a tendency towards elongation. The more lateral the light, the more is the petiole lowered, until, perhaps, it descends below the horizontal (fig. H_2), and when in such a position the upper pulvinus is curved as a strut under the hinge. The more the petiole descends below the horizontal the more obvious is this strut.

The fourth leaf is the sun-leaf, which has been mentioned. It has a shorter petiole than the shade-leaf, so much so that on a stem which has climbed through shading vegetation to a position in the sun where it rests on the top of the competing vegetation, there may be an abrupt shortening of the petiole by 10–20 per cent. The lamina, too, may be proportionately shortened, and it is commonly of a deep green. But the chief character is the uprising of the auricles, whereby the shape of the lamina is made to approach that of the spout of a jug (fig. H_3). All the primary nerves of such a leaf have a curvature so as to be concave towards the back of the leaf, the decurving midrib makes the apex of the spout, while the auricles rise up and open out above the top of the petiole. In sun-leaves the assimilatory tissue tends to be bullate, and in common with the raising of the auricles, this bullation causes a considerable part of the surface of the lamina to be presented obliquely to the sun's rays. A foundation for this bullation is laid down very early in the young leaf, for the nerves carry the assimilatory tissue high in a way which must lead to upward extension as it becomes fuller than its space between the nerves. Powerful light, by arresting the growth of the framework supplied by the nerves (sun-leaves are relatively shorter than shade-leaves) directly promotes this bullation; and light, arresting the back of these nerves more than the face, produces the curvature which leads to the spout-form. The curvature is quickly fixed in growth, so that plasmolyzing salts do not undo it. But plasmolysis weakens the power of the hinge to hold up the auricles. Accepting turgidity as a precursor of growth, it is not surprising that a delay in turning turgidity into growth should be detected in the part of the lamina where the youngest tissue is, namely at the base. The upper pulvinus in the sun-leaves tends to be straight, just as the upper pulvinus of a leaf at the ground in shade. In the sun-leaf the straightness of the abaxial side of the upper pulvinus may possibly arise from the same cause as the arrest of growth in the lower surface of the primary nerves.

In brief, the several leaf-forms after the seedling stage are modifications due to the direction and strength of light, and the behaviour of the sun-leaves shows full sunlight to be more than *Tamus* seeks.

H

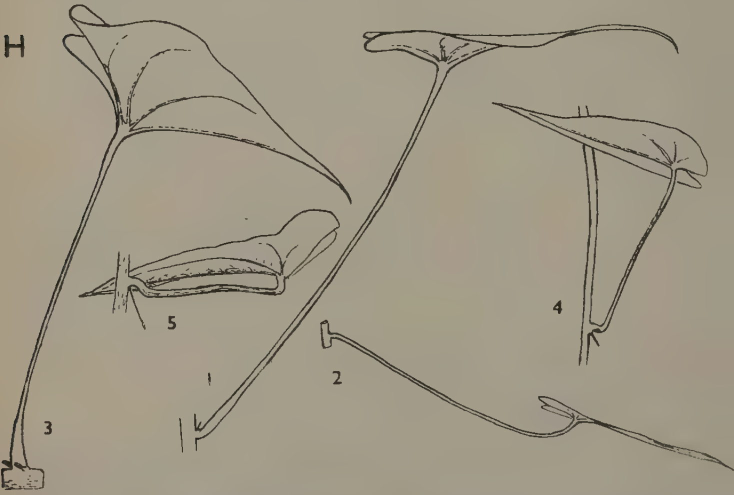


Fig. H.—1, a leaf from a climbing stem in considerable shade, showing that the lamina is flattish ; this particular leaf was obtained where diffused light came to it through the top of a thicket. 2, a leaf from a climbing stem in considerable shade, showing its flattish lamina and the strut formed by the upper pulvinus, the light being from the side. 3, a sun-leaf, as described in the text. 4, a leaf from a stem which had been inverted, and which was in the process of correcting its position by a somersault in which the lamina was directed at the stem and pushed past it. 5, a leaf on a stem which was inverted by successive stages in an attempt to ascertain how much curvature could be produced in the upper pulvinus. All $\times \frac{1}{2}$.

But there is something which may be called a want of power of proportionate elongation in leaf and stem of the seedling, of a nature not yet recognizable, which scarcely seems connected with light.

The angle of the hinge.—Fig. J supplies the lines on which the following paragraph is based. It represents a leaf which is neither an extreme sun-leaf nor an extreme shade-leaf, but the commonplace intermediate. The point *a* is the junction of the petiole and the lamina, the point where the vascular bundles passing between the petiole and the lamina have their cross-ties, the point where, indeed, an arrest of growth with great power is inserted very early—say at 3 mm.—in the history of the young leaf. The point *b* is at the union of petiole and pediment, and any line *ab* connecting the two shows the measure in which the petiole of a given leaf deviates from a straight line. The line *ac* is ruled from *a* down the upper pulvinus by using its upper few mm., and consequently the angle *bac* gives the curvature of that pulvinus. The line *ad* is ruled over the lowest few mm. of the midrib, and the angle *cad* is, therefore, the angle of the hinge and can be compared with the angle *bad*, which is the angle made by the petiole as a whole with the base of the lamina. The line *ae* connects the point *a* with the leaf-tip, and the angle *bae* is the angle of the petiole as a whole with the lamina as a whole. Rigid accuracy is not attainable in ruling lines *ac* and *ad*, but the approximation is useful. If a leaf under examination be cut with scissors along one edge of the midrib, it is a simple matter to lay it with the cut edge against a sheet of paper and to trace with a pencil the lines of the petiole and lamina, and then to rule *ab*, *ac*, *ad* and *ae*. From a considerable number of diagrams so made, using leaves from hedgerows of my neighbourhood in Surrey, I find *cad* to vary between 80° and 160°, with a concentration between 120° and 140° and a mean about 130°. If the angle *bad* should be very wide, as it is in such leaves as H_2, the curvature of the upper pulvinus enables the angle *cad* to approach 130°. The curvature of the upper pulvinus shortens the distance to which the petiole can stretch out the leaf, and that it should occur where stretching is a main object suggests how insistent the hinge is in resistance to an approach of the angle towards 180°. I am calling an angle of about 130° for this point of union of petiole and lamina an angle of ease. It is autotropic.

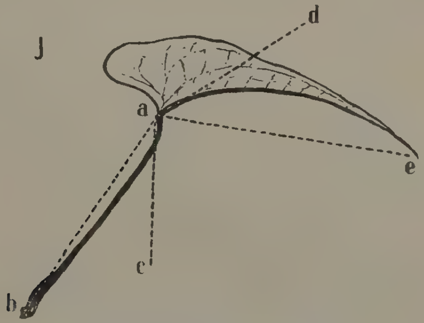


Fig. J. (Explanations in the text.)

To illustrate it more fully, the usual course of development of pose may be considered in a leaf produced in good light on the upper side of a stem which, having climbed successfully to the top of its support, sprawls over it. Using the clock-face and imagining the stem in section as a clock-dial, this leaf may be said to arise at 12 o'clock. As it grows, the petiole lifts the lamina which had started life inverted as to gravity and as to the light, and turns it over so that, with geotropism met, its face may get the light. Position K_0 of the figure would seem able to satisfy this need, but is not produced or, if produced, is not maintained ; instead, the leaf passes to position K_3, wherein the angle of ease is more or less 130°, for the conflict between the demand of the lamina to be lifted towards the light and the stretching of the angle has been settled by a driving of the petiole beyond the upright to an obliquely inclined pose, with the lamina it bears pointing down the stem. The part of the leaf required to yield has been the other angle, i.e. the ontogenetic angle between petiole and stem, and the agent the adaxial side of the lower pulvinus ; at the same time the upper pulvinus has been allowed to remain straight, or, if we like, to obey its autotropism.

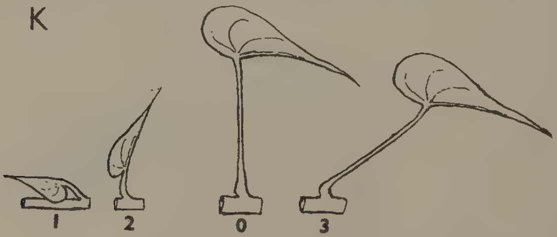


FIG. K.—1, a leaf expanding from a horizontal stem on its upper side, and 3, the ultimate position attained. 2, a stage in the growth which is passed through in attaining the position, but 0, one which is not realized because the angle of the lamina on the petiole is not an angle of ease.

In contrast in the shade-leaf of fig. H_2, in order that it may attain its pose, the adaxial side of the lower pulvinus has increased growth as that of the sun-leaf of K_3, and the abaxial side of the upper pulvinus has also increased growth, and in this way the action is not restricted to one side of the petiole, but suggests an independence of the pulvini. Later in this paper, where fig. R is considered, the position of the curvature in the lower pulvinus of a deflected leaf is discussed.

If the reader will now turn fig. K through 90°, he will readily appreciate how the leaf figured earlier as H_2 got its pose, for by turning the figure he has made the horizontal stem into a climbing stem.

Incremental growth on the flanks of the upper pulvinus.—Before the lower pulvinus is discussed, in order to complete in some degree the account of adjustments which the upper pulvinus makes, its capacity of growth on its flanks may be considered. Fig. L illustrates this capacity. There are pulvini of two leaves in the figure, the one with the curvature increased downwards, the other with the curvature increased upwards. The first leaf was posed without any canting ; the second with canting. As the dotted lines indicate, the curvature of the first was about twice as great in the lower 5 mm. than in the upper 5 mm. The leaf of the second, to get the lateral light, was canted to the extent of 45° (the line *rs* gives the angle). From the point *a*, where there is a dotted line ruled across the top of the pulvinus, there are also two other dotted lines, which indicate the direction of the two margins and show that the canting was unequal in the two sides of the lamina, the upper part of which was rather flat, as a shade-leaf is, and the lower part arched, as a sun-leaf is. The canting was divided between lamina and pulvinus, the major part effected by the lamina, the balance by the upper 5 mm. of the pulvinus: the taking up of the canting by the lamina involved unequal growth on the two sides of the hinge, i.e. in tissue adjacent to the point *a* which, lying between the hinge and that part of the pulvinus which took up the rest of the adjustment, may be regarded as the focus of such adjustment. An examination of a large number of canted leaves indicates that it is typical for *a* to be the focus when the petiole ascends in a normal way; but when, for some reason, the petiole does not ascend in a normal way (e.g. fig. L_2), the entire adjustment may be within the petiole. Conversely, there are found cases with the entire adjustment within the hinge; these are part of the class of cantings wherein the petiole ascends normally.

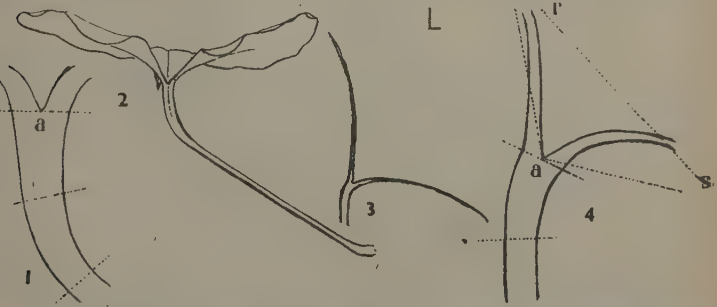


FIG. L.—1, the upper pulvinus of a leaf, ×2½, in which the curvature to the side increased downwards, ruled with lines 5 mm. apart. 2, that leaf, showing its pose, ×½. 3, a section through a canted leaf, ×½. 4, the upper pulvinus of this canted leaf, showing the curvature to the side increased upwards.

It is usual to find torsion associated with those adjustments of pose which are contrived within the petiole.

Canting is very common. Out of 120 leaves taken from a tangle of *Tamus* stems sprawling over a low bush, 65 per cent showed some canting: out of 167 leaves taken from a pendent tangle of stems, 72 per cent showed some canting: and out of 196 leaves taken from a plant in a shaded place backed by palings, 70 per cent had a canting. Such abundance doubtless arises from the chances in Nature being so enormously against the two halves of any lamina being under exactly equal conditions of light, even if structurally exactly paired, the leaf meeting the inequalities by canting its lamina.

No canting of the leaf at a very early age, as figured as E_6, need be permanent ; and there is evidence of an autotropism in the upper pulvinus, or, may we say, of an autotropism extended from the shaft into the upper pulvinus, which leads to a straightening of the pulvinus if the requirements of the lamina can be met by growth in the hinge. And this happens with curious results. Fig. M shows the forms of four injured leaves, taken from hedgerows, in which the hinge by growth had restored an approximate equipoise of the remnant of the lamina and the upper pulvinus was straight.

M

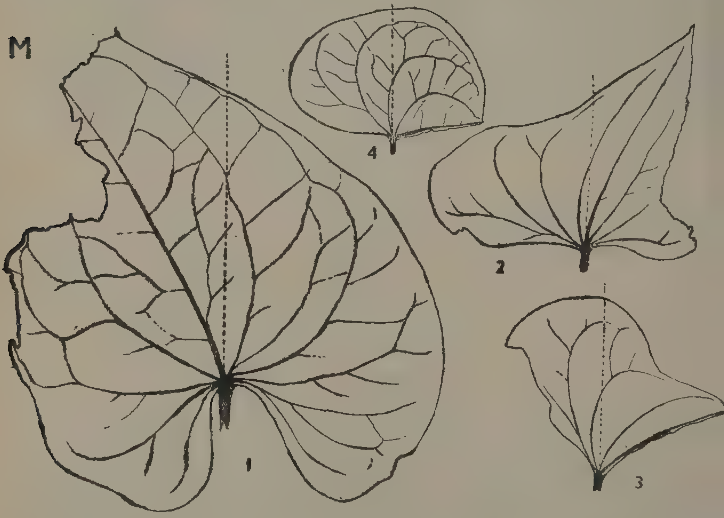


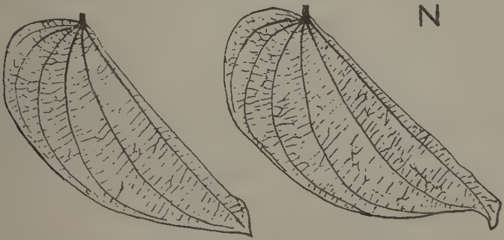
Fig. M.—Four injured leaves with the midrib out of line with the petiole, the upper pulvinus of which was straight. A broken line continues the direction of the petiole, and the superficies of the lamina on either side of these dotted lines were :—

On the left (in sq. cm.) leaf no. 1	84	67 on the right.
2	19	19
3	10	11
4	10	10

The injury to leaf M_1 was such that, when found, the superficies on the less injured side of the midrib was 94 sq. cm. and on the more injured side 57 sq. cm. ; but the displacement of the lamina had been such that the areas on either side of the dotted line had become 67 and 84, i.e. the displacement had more than compensated the loss (see the data in the legend under fig. M). Leaf M_2 had sustained injury entirely on one side (the kind of injury that the Hemipteron *Bubulcus* causes), and similar growth of the hinge had moved the lamina sideways, so that the superficies on either side of my dotted line had become 19 sq. cm.

aves M_3 and M_4 had lost one-half of the lamina by a tear along the ie of the midrib, and the remaining half had come to a balanced position the end of a straight (? straightened) pulvinus. These having been igerow leaves, I do not know their exact history; but I judge that loss of the half of the lamina had taken place very early, because perimental mutilations of a similar nature which I have made have had ser effects in the shortening of the length of the lamina in proportion the growth of the remaining auricle which has had the food of two. another year I hope to experiment with mutilations where I can control ht—that is, in my own garden.

ig. N is from an experiment in my garden on leaves of *Dioscorea uca* fully exposed to diffuse light in the morning and to full sunlight rough the afternoon. The leaves were mutilated when in the stage E_6, and the drawings made at the end of autumn, when the leaves re about to die. By growth in the hinge the midrib had been inclined the mutilated side so much further than was needed to place an equal ea on each side and the superficies on either side of a line prolonging the ne of the upper pulvinus was—the leaf on the left 11 sq. cm. on the injured side to 14 sq. cm. on the other; and the leaf on the right, ½ sq. cm. on the uninjured side to 16 on the other. Let it be fully nderstood that the displacement is invariably towards the side injured, this indicates where the amount of auxin is in deficit. It sometimes ppens that the distal part of the pulvinus is straight under an injured mina, with a curve occurring in the lower part, a condition still under perimental study.



N

N.—Two mutilated leaves of *Dioscorea glauca* five months after the mutilation had taken place, the stage at which it was done having been that of E_6. The upper pulvinus had grown straight: the hinge had responded to the upset of the equipoise of the lamina; but the disturbed centre of gravity had been moved too far to the right to re-establish an equipoise.

The lower pulvinus.—The divergence in *Tamus* is variable around 3 in old plants; and most of its leaves, since they are produced on sides of the stem, whether it be climbing or horizontal, are in need adjustment of pose in order to make the best of the available light he stem may be twisted a little, now in one direction, now in the other, ut that is of no moment, for it is not twisted to the advantage of the leaves; and it may be said categorically that the lower pulvinus scarcely ever escapes a demand that some adjustment of the pose of the lamina shall be made by growth in it. Its responses are now in one part, now in another, in a way which shows that it is far from being a simple similitude of a ball-and-socket joint. Firstly, as to the parts which respond: these are illustrated here by four figures (O, P, Q and R),

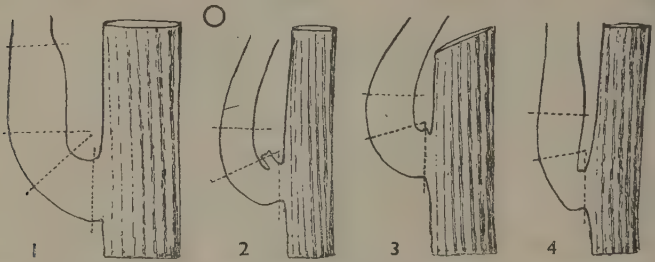


FIG. O.—Four pulvini wherein the curvature was median and abaxial, and driven to the very base, but not so completely in O_1, the pulvinus of a large leaf, than in the others; but in this the distal 5 mm. was not at all curved. In O_2 the radius of curvature in the lowest 2·5 mm. was 3·5 mm., and increased in the next 2·5 mm. to 8 mm. In O_3 the radius of curvature in the first 2·5 mm. was 3·2 mm. increased in the next 2·5 mm. to 11 mm., and there was a slight crumpling of tissues in the axil. In O_4 almost the whole of the curvature was in the lowest 2·5 mm., and there was distinct crumpling of the surface in the axil.

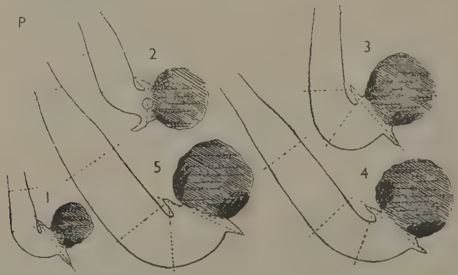


FIG. P.—Five pulvini wherein the curvature was driven to the base on the flanks. They are numbered by the size of the stems, this being a general index to the length of the pulvinus. In P_1, where the pulvinus was about 4 mm. long along its middle line, the whole curvature was in the lowest 2½ mm., the radius being just under 2 mm. In P_3 the same was the case, the radius being about 3 mm. In P_3, the radius of the lowest 2½ mm. was 3 mm., that of the next 2½ mm. about 3·5 mm., above which for another 5 mm. the pulvinus was straight. In P_4, with a pulvinus 12 mm. long, the radius of the curve of the lowest 2½ mm. was 3·2 mm., of the next 2½ mm. 4·8 mm., and the rest of the pulvinus was straight. In P_5, a pulvinus similar to the last, the radius of the curve of the lowest 2½ mm. was 3·5 mm., of the next 2½ mm. 4·2 mm., the further 8 mm. of the pulvinus being straight.

one for each of the parts of the pulvinus mainly affected. The drawings for these figures were made in the following way: suitable pulvini were selected, divided medially and placed on a millimetre grid under a dissecting microscope; the medial division was done that they might lie flat: then outline drawings at a magnification were made on paper squared in millimetres, and after they had been made, dotted lines were ruled on the drawings at points 2·5, 5, 10 and 15 mm. from the base, with the intention of making evident the radius of the curvature.

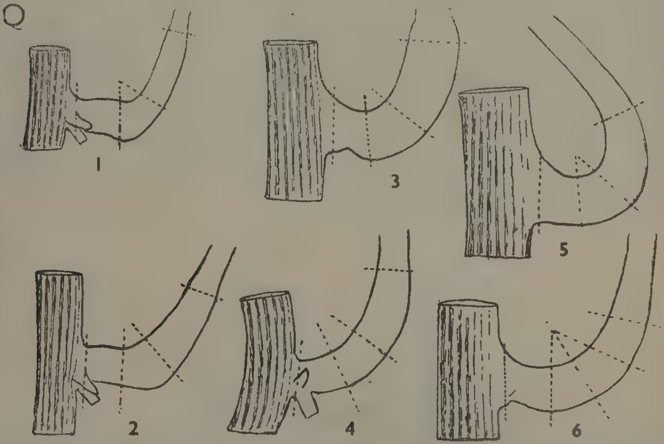


Fig. Q.—Six pulvini of leaves from pendent stems, showing that the location of the maximum curvature on the adaxial side tends to be above the very base. In Q_1 the lowest 2½ mm. are not curved, but the next 2½ mm. are curved with a radius of 3·8 mm., the rest of the pulvinus with a radius of more than 12 mm. In Q_2 the pulvinus exhibited the same features, the radius of the curve of the second 2½ mm. being about 5 mm. In Q_3 the first 2½ mm. were but very slightly curved, the next with a radius of 4·5 mm., the rest of the pulvinus with a radius of 12 mm. In Q_4 there was a little curvature to the base, the radius of the first 2½ mm. being 6·5 mm.; the curve increased in the next 2½ mm., so that the radius was 6 and diminished over the next 5 mm., so that the radius was 10. In Q_5 the curve with a radius of 16 mm. in the first 2½ mm. increased to a radius of 5 mm. in the next 2½ mm., and remained almost the same through the next 5 mm. In Q_6 curvature arose in the first 2½ mm., which was maintained through the next 2½ mm., diminishing through the following 5 mm. almost to have disappeared in the remaining uppermost 2 mm. before the pulvinus passed into the shaft.

Fig. O gives four pulvini in which the response was median and abaxial. In three out of the four the shortest radius was in the lowest 2·5 mm. In the remaining pulvinus, O_1, a pulvinus which carried a larger leaf than the others, it was in the lowest 5 mm.

Fig. P gives five pulvini on stems in section, numbered according to the size of the stem, these pulvini having lateral curvature. The dotted lines show that the maximum curvature is basal, as in the pulvini in fig. O.

Fig. Q illustrates curvature on the adaxial side and was prepared by the use of leaves from stems which had been rendered pendent, the intention of selecting these being to obtain the effect of the greatest possible stimulation. The reader will observe that the maximum curvature is not now at the very base, but a little above it.

Fig. R illustrates curvature also on the adaxial side, but of a different nature to that in fig. Q. None of the pulvini drawn are of leaves which had righted themselves after inversion, but of deflexed leaves from climbing or horizontal stems, and the curvature is in the distal part of the pulvinus close against the base of the shaft.

By these four figures, O, P, Q and R, it is indicated that curvature on the abaxial side tends to be more basal than on the adaxial side, and that two kinds of curvature appear on the latter side, the one, that of fig. Q, moving the lamina more than the other, that of fig. R. It seems possible that Q is a response to a bigger stimulus than R. On searching the hedgerows where *Tamus* grows, P will be found the commonest and after it R, not because they are the more easily produced, but because they are the more needed.

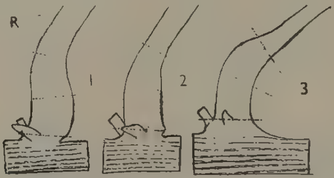


FIG. R.—Three pulvini of deflexed leaves of climbing stems, showing the maximum curvature to be distal.

That the curvatures of O and P should be so decidedly basal is interesting in connection with the direction from which the stimuli come; for these must penetrate the upper part of the pulvinus, which they reach before they reach the basal part; and this is as if the autotropism of the shaft had some power on the abaxial side over the adjoining part of the pulvinus. But all that is certain is that the pulvinus is differently responsive dorso-ventrally. With the curvature of R distal and that of O basal, it is possible for both to occur in the same pulvinus.

The reader needs to be informed here that the base of the petiole is not flush with the surface of the stem. If the development of a leaf be followed, the bud in its axil is first observable on the axis (see Journ. Bot. 1939, p. 326); that later it seems to arise on the petiole (cf. fig. P_2 here) is due to growth of the pediment (Grégoire's soubassement foliare), which carries the axillary bud and the stipule-like emergences outwards.

Curvature, as in fig. P, is always accompanied by torsion, to explain which fig. S has been prepared. S_1 is a leaf produced so that it is laterally illuminated; it may be a leaf at 3 or 9 o'clock on a horizontal stem or a similarly illuminated leaf on a climbing shaded stem. The lateral light starts growth in the flank of the lower pulvinus and the lamina is lifted (S_2), but does not remain sideways to the light, for invariably this kind of growth throws the lamina over face upwards (S_3).

Laminae to the right are thrown over in one direction, laminae to the left in the other: the effect is the same.

It is not difficult to suggest how this happens, although full proof has yet to be obtained. The explanation suggested is that resistance of the tissues produces the throw-over. If the reader will turn to fig. G_3 (p. 262) he will observe that growth which is lateral is above the level of the larger bundles and below the level of the smaller. Let fig. G_3 be turned through a right angle and the pulvinus it represents is in the position of that in fig. S_1: growth on the surface which the turning has made below may well find much less resistance to the right than to the left: therefore torsion.

The ultimate or light-fixed position of a leaf with torsion in the lower pulvinus.—Herein horizontal and climbing stems differ. S_3 represents what happens in a horizontal stem; the leaf stands out with its midrib more or less at 90° to the stem, being at the same time subject to a determination of level as a matter of accommodation between the effect of light on the lamina and the angle of ease, and it remains at that angle. The leaf on a climbing stem which, with torsion aiding it, has moved round to 90°, does not have its movement arrested there, but allows its apex to fall until it points earthwards. This I attribute to its weight. A leaf held out on a horizontal petiole sideways from a climbing stem is the rarest of objects, and it requires no imagination to realize that the position would be one of strain. Accordingly when the leaf happens to approach such a position, adjusting movements which give way to the strain are favoured, and by degrees the pose which is exhibited so freely in fig. A comes into being.

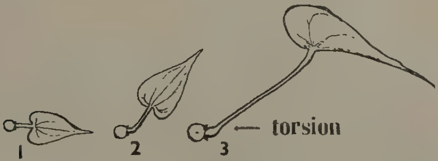


FIG. S. (somewhat diagrammatic). 1, a leaf in the stage of C_6 arising so that it is laterally illuminated. 2, its response to the light; and 3, the same when torsion has supervened.

Leaves brought round from the back of a stem, i.e. from altogether away from the light, arrive at the same position, i.e. with the apex pointing earthwards, but with a variation in the angle which is in itself an indication that the response is not purely psychic.

The shaft of the petiole.—It has been stated earlier (p. 256) that the straightening of the young petiole in the passing from stage C_6 to C_7 is sometimes overdone: that leads to a convexity on the abaxial side of the shaft. Such a convexity is always slight.

The shaft does not curve towards one flank or the other, and, though petioles may be found seeming at first sight to be so curved, they are not really so, but are misshapen petioles with dorso-ventral convexity twisted out of plane. I figure nine petioles in fig. T which appear to be curved sideways, but eight of them were not: and at the letter *t* in each the groove of the face of the petiole dipped to the side, so that the curvature seen was actually in the dorso-ventral plane of the petiole. It may be noted that the position of *t* varies a little.

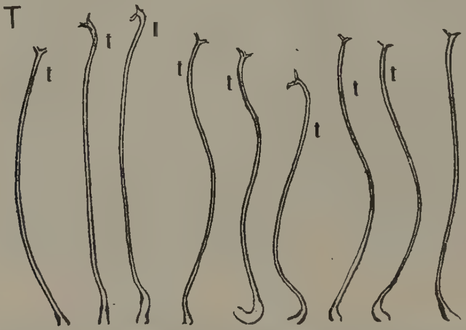


FIG. T.—Nine petioles, × ⅓, eight of them appearing to be curved to the side, but this appearance arises from torsion combined with curving in the dorso-ventral plane. The torsion is in one direction at the base and is counter-torsion at the apex.

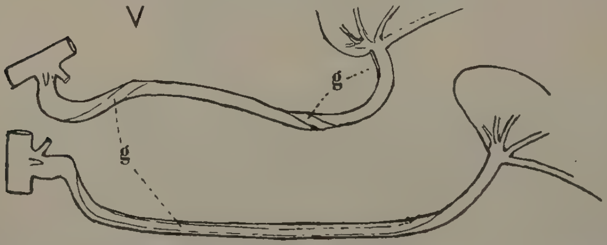


FIG. V.—Two petioles thrown out of straightness and twisted as the result of fixing the laminae immovably in a false position : *g–g* the groove which belongs to the side of the petiole normally uppermost.

Such misshapen petioles are abnormalities, and the like can be created by fixing a young leaf in a false position so firmly that it cannot be turned. Fig. V shows what happens. It is interesting to observe that the effort to correct the position which was concentrated low down in the petiole had force enough to impose counter-torsion at the other end of the petiole. The forcing of this counter-torsion on the upper end is reminiscent of the counter-spiral forced on the distal part of an attached tendril of *Bryonia* or *Vitis*.

That it is mechanically induced supports the contention (p. 273) that torsion in the lower pulvinus is mechanical.

The ninth petiole in fig. T was exceptional in exhibiting genuine slight lateral curvature produced without torsion. It has been inserted into the figure to show that such may occur.

The powers of adjustment.—The lower pulvinus, working as a ball-and-socket joint, can point the lamina through the greater part of a half-sphere. Its dorso-ventral structure produces a small measure of limitation; but the adaxial face and the abaxial back are almost equally ready to do what is required of them. In fig. W two leaves are represented from the same stem of *Tamus*, a stem which was uncoiled from its support and fixed in an inverted position. The lamina of one leaf was returned to a correct position by a somersault, passing through the stage of fig. H_4 in the process, with the apex driven at and pushed past the stem. The second lamina, for an obscure reason, was returned by another course, as indicated, to a correct pose, though with a slight abnormal curve in the petiole. Other leaves on the same stem corrected their position by a combination of growth on the adaxial side of the lower pulvinus with torsion through upwards of 180°, in which case the growth of the lower pulvinus had only half the work to do which it did in W_1. I do not know why three neighbouring leaves should take three different paths to the same end, and can but suggest that almost undetectable initial differences account for the path taken.

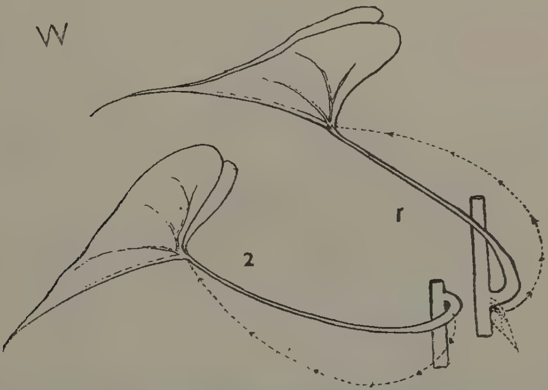


FIG. W.—Two leaves from a stem made pendent so that they had their faces earthwards. Leaf no. 1 returned to a correct position by a somersault through 180°; leaf no. 2 by movement under its attachment and finished with a curved petiole.

The power of the upper pulvinus to move the lamina is less than that of the lower, but extreme excitation can make it curve on the adaxial or the abaxial side through 90° (see figs. H_2 and H_5). It seems much less able to curve by growth in the flanks.

The power of the hinge is not well defined. Canting partly by the pulvinus and partly by the hinge may reach 80° on rare occasions, but is usually much less.

Torsion in the petiole may extend to 180°.

It requires a big jolt to call out the full measure of response in any case, and it is interesting that there should be so much power held in reserve for occasions which so rarely arise.

The stimuli which lead to the pose of the leaf are heliotropic, almost to the exclusion of geotropism. They work manifestly by differences, trying to bring the worst illuminated part of the lamina up to or towards the best, and there are infinite chances for differences, with the complication that the optimum illumination is apparently less than the maximum possible.

Autotropism, or the undoing of the work of stimuli, seems a real force in the petiole.

SUMMARY.

The young leaf of *Tamus communis* passes through the stages given in fig. C to a time when it becomes geotropic and heliotropic. The corresponding stages in *Dioscorea glauca* are given in fig. F. All these stages are ontogenetic. But ontogenesis is as yet incomplete, and along with waves of growth, basipetal in the lamina, there is a spread of rigidity in the petiole from the centre towards its ends, both ontogenetic phenomena. These ends, so long as they remain able to grow, obey stimuli originating in the lamina and communicated through the vascular tissues by an auxin from the part of the lamina which is at a disadvantage to that part of the petiole where growth decreases the disadvantage. It is convenient to regard the rigidity of the shaft of the petiole as promoted by an autotropism (p. 256); and to think that it is the spreading of this autotropism into the pulvini from the shaft which slowly drives curvatures (i) out of the upper pulvinus until any adjustment which had been for a time in the pulvinus has been transferred to the lowest part of the lamina (fig. M), and (ii) downwards as far as possible in the lower pulvinus provided that the curvature is on the abaxial side (fig. O) or on the flanks (fig. P); but it does not drive the curvature down in the same degree in the lower pulvinus on the adaxial side (figs. Q and R). Therefore the lower pulvinus is not a simple organ Moreover, the anatomical structure of the lower pulvinus is such dorso-ventrally that it causes torsion to accompany growth on the flanks (fig. G_3, for the anatomical structure, and fig. S for the effect). Torsion occurs also in the upper pulvinus (p. 259). The dead weight of the leaf favours the enduring of movements pointing the apex towards the earth (p. 273). The angle which the lamina makes with the petiole is limited by autotropism (fig. J), and the upper pulvinus becomes an accommodating strut (fig. H_2), and/or the lower pulvinus takes on increased growth on the adaxial side (fig. K_3), in order that the angle may be within its limits. Growth in *Tamus* is promoted by shade: shade-leaves become elongated both in lamina and petiole, with the result that there is an induced heterophylly. The assimilating parenchyma is slack and the tissues about the primary nerves of the lamina spread the blade; it is evident that the primary nerves respond to the effect of the auxin as well as the petiole. The shape of a sun-leaf (like the spout of a jug) shows that the weaker of the primary nerves (fig. H_3) are made to rise upwards when the stimulation for growth is weakened in sunlight, whereas the midrib does not. This is contrived by pressure of growth at the base of the blade, and is a turgidity phenomenon, the turgidity which is operative being that which pushes the primary nerves apart (cf. Journ. Bot. 1939, p. 325; and see p. 263 above), and it is unnecessary to suspect that there may be any heliotropic difference, even in degree, between the different nerves.

The characters here established for *Tamus communis*, the Black Bryony, as far as they are shared by *Dioscorea glauca*, are probably general throughout the climbing Dioscoreaceae; and in this paper the organization of the petiole has been described sufficiently to enable a comparison to be instituted with that of other families.

A KEY TO THE AUSTRALIAN SPECIES OF CAREX (CYPERACEAE).

By E. Nelmes.

Since January 1941 I have had the opportunity to study the Australian *Carices* represented in the Kew Herbarium, and have prepared detailed descriptions of them and a tentative key. As it is not likely that a full account can be printed during the war, the key is herewith published in advance.

My studies have been carried on under considerable difficulties, since only about half of the types of the Australian species—those possessed by Kew—have been available, and although access has been possible to the whole of the New Zealand, Malayan and African material of *Carex* in the Kew herbarium, and to the Indian and Chinese types there, most of the European, American and remaining Asiatic specimens have not been available. The handicap caused by the absence of this material will be realized when it is mentioned that of the 29 Australian species recognized by Bentham in the 'Flora Australiensis', eight were considered by him to be conspecific with, and four others to be closely allied to, European species; a number of taxonomic points, therefore, still await a definite decision. It will no doubt be possible to improve the key when the full revision of the Australian *Carices* is published.

It should be mentioned that the very tentative order of the species in the enumeration which follows the key, though departing radically from Kreczetowicz's arrangement in the 'Flora URSS' (III, 1935), in so far as the plants of the two areas are comparable, is nevertheless based on his view (expressed in Journ. Bot. URSS, XXI, 1936; translated by Mr. H. K. Airy-Shaw) that *Carex* had a tropical and probably Malayan origin. Mr. Airy-Shaw's experience of the Malayan flora in general has led him to views which tend strongly to confirm that of Kreczetowicz on *Carex*. The descriptions of the sections into which I have grouped the species, and other details of classification, must be excluded from this list and reserved for publication in the forthcoming larger work.

Finally, a few special comments on the species seem desirable.

C. Rafflesiana Boott is not represented at Kew, and is included on the authority of Kükenthal (Engl. Pflanzenreich, 1909), who cites a specimen in the herbarium of the Melbourne Museum collected by 'St. Johnson' on Mt. Bartle Frere, Queensland.

There are specimens at Kew from Lord Howe Island, varietally and possibly specifically distinct from *C. brunnea* Thunb., which are not included here, as they may be referable to *C. Hattoriana* Nakai, the type of which is not at present available.

Certain specimens from the southern parts of Australia which are related to *C. pumila* Thunb. have not here been taken into account because the material is inadequate for precise placing.

It has already been mentioned how difficult it is, in the absence of the European material, to deal justly with those Australian species which are either conspecific with European species or closely related to them. These species are: *C. fascicularis* Soland. ex Boott, *C. cataractae* R. Br., *C. canescens* Linn., *C. divisa* Huds., *C. echinata* Murr., *C. curta* Gooden., and *C. cephalotes* F. Muell. Kükenthal considers that none of these (omitting *C. divisa*, which has been recorded for Australia since the date of his monograph) is specifically separable from the corresponding European species; but here I have ventured to treat three of them—*C. fascicularis*, *C. cataractae* and *C. cephalotes*—as specifically distinct from the European *C. Pseudocyperus* Linn., *C. flava* Linn. (and its near allies), and *C. pyrenaica* Wahlenb. respectively. The remaining four exhibit only slight differences from their European counterparts, and for the present at least I follow all previous authors in including them under their original names.

Key.

Spike 1, androgynaeceous; utricles smooth on the margins:

Staminate part of spike as long as or longer than the pistillate part and not less conspicuous .... 45. *capillacea.*

Staminate part of spike from slightly to much shorter than the pistillate part, always inconspicuous and usually so very inconspicuous that the spike appears to be wholly pistillate:

Spike 7–12 mm. long, pistillate part many-flowered; lowest scale normal .... 43. *cephalotes.*

Spike 4–5 mm. long, pistillate part about 3–6-flowered; lowest scale bracteal, exceeding the spike .... 44. *Archeri.*

Spike 1, gynaecandrous; utricles minutely setulose on the margins: depauperate states of *C. Raleighii*, *C. hebes*, and *C. inversa*, which see below.

Spikes more than 1 (sometimes reduced to 1 in depauperate states of *C. Raleighii*, *C. hebes*, and *C. inversa*, and falsely unispicate in *C. paupera*):

Stigmas 3; utricle more or less trigonous, not plano-convex:

Utricles rhomboid-lageniform .... 9. *breviscapa.*

Utricles not rhomboid-lageniform:

Spikes on ascending stems from basal leaf-axils on a short undeveloped shoot .... 8. *cryptostachys.*

Spikes numerous, in branched panicles terminating an erect stem:

Secondary panicles mostly binate; female scales ferrugineous; utricles hispidulous above on the nerves and margins .... 1. *Rafflesiana.*

Secondary panicles solitary; female scales not ferrugineous; utricles glabrous except on the margins:

Utricles ellipsoid-obovoid, subinflated, obscurely trigonous; scales castaneous above; leaves about 5–9 mm. broad .... 2. *Dietrichiae.*

Utricles ellipsoid, not inflated, distinctly trigonous; scales whitish; leaves about 7–17 mm. broad .... 3. *Fleckeri.*

Spikes in fascicles of 1–5 at nodes on an erect stem:

Female scales whitish with a green central stripe, 4–5 mm. long, 1·25–1·5 mm. broad; utricles distinctly nerved on the ventral face, whitish-setulose from near the base to the apex; spikes lax-flowered, 3–4 mm. thick in mature fruiting stage, all androgynaeceous, uppermost with a rather long male apex .... 4. **Hubbardii.*

Female scales castaneous to light reddish-castaneous, 4–5·5 mm. long, 1·5–2 mm. broad; utricles nerveless on the ventral face, setulose only on the margins above and on the faces near the apex; spikes lax-flowered below, rather dense-flowered above, 3–5 mm. thick in mature fruiting stage, upper gynaecandrous (sometimes with male apices), uppermost with a long, usually very long, male basal part, lower gynaecandrous or female .... 5. *longibrachiata.*

Female scales yellow-castaneous, 5–7·5 mm. long, 2·5–4 mm. broad; utricles nerveless on the ventral face, glabrous except on the margins, which are setulose near the apex; spikes dense-flowered, 5–8 mm. thick in mature fruiting stage, uppermost 1–3 (–4) wholly male, rarely with a few female flowers in the terminal spike, remainder wholly female or with male bases and/or apices .... 6. †*lynx.*

Spikes solitary at nodes on an erect stem:

Utricles more or less pubescent .... 10. *breviculmis.*

Utricles glabrous, except sometimes on the margins of the beak:

Utricles corky, with impressed nerves:

Stems free from the leaf-sheaths for a considerable distance; male spikes about 7–13; female spikes mostly spaced at some distance from one another; female scales purplish-brown to castaneous; utricles 4–5 mm. long, golden-reddish- and blackish-splashed; near the sea but apparently not on sandy shores .... 11. *Bichenoviana.*

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* **Carex Hubbardii** *Nelmes*, sp. nov.; affinis *C. longibrachiatae* Boeck., sed spicis magis laxifloris omnibus androgynaeceis, squamis femineis albescentibus, utriculis albescenti-setulosis ventre distincte nervosis, praecipue differt. Type: *Hubbard* 5211. Mt. Mistake, Queensland.

† **Carex lynx** *Nelmes*, sp. nov.; affinis *C. longibrachiatae* Boeck., sed spicis crassioribus densifloris 1–3 superioribus vulgo masculis, squamis femineis latioribus, praecipue differt. Type: *Archer*. Tasmania.

  - Stems usually mainly hidden in the leaf-sheaths; male spikes 1–4, usually 2–3; female spikes usually approximate or subapproximate; female scales castaneous to reddish-castaneous; utricles (5·5–) 6–7 mm. long, mainly stramineous but sometimes with castaneous or brown splashes; on sandy shores...... 12. *pumila.*
- Utricles neither corky nor with impressed nerves:
  - Leaves septate-nodulose:
    - Terminal spike male:
      - Beak of utricle with stiff, slender teeth which are about 1 mm. long and smooth inside.............................. 13. *fascicularis.*
      - Beak of utricle with membranaceous, stoutish teeth which are 0·2–0·3 mm. long and ciliolate-hispidulous inside... 15. *conspicua.*
    - Terminal spike composed of both male and female flowers .... 14. *alsophila.*
  - Leaves not septate-nodulose:
    - Male scales cuneate or oblong-cuneate, with an awn as long as or longer than the rest of the scale........................... 23. *Brownii.*
    - Male scales neither cuneate nor oblong-cuneate, when awned the awn shorter than the rest of the scale:
      - Terminal spike gynaecandrous .... 24. *canescens.*
      - Terminal spike male (often androgynaeceous in *C. cataractae*):
        - Bracts sheathless; beak of utricle truncate, erose, and swollen at the apex.. 22. *lacistoma.*
        - Bracts, or at least the lower ones, sheathing; beak of utricle not swollen nor truncate but more or less bidentate or notched at the apex:
          - Utricles minutely notched at the apex of the beak, minutely and densely papillose .... 25. *neurochlamys.*
          - Utricles bidentulate or bidentate, not papillose:
            - Utricles distinctly yellowish when mature; terminal spike often androgynaeceous .... 21. *cataractae.*
            - Utricles not yellowish; terminal spike male:
              - Utricles coriaceous; apices of leaves and bracts becoming withered and circinnate .... 20. *tasmanica.*
              - Utricles membranaceous; apices of leaves and bracts not circinnate:
                - Leaves 3–9 mm. broad; female spikes 6–10 mm. thick at maturity; beak of utricle 0·7–2 mm. long, teeth 0·3–0·5 mm. long:
                  - Utricles (4–) 5–5·5 mm. long, strongly many-nerved, beak subterete and about 1–2 mm. long .... 16. *Gunniana.*
                  - Utricles 3–4 mm. long, finely many-nerved, beak flattish and about 0·7–0·8 mm. long .... 17. *Blakei.*

Leaves 2–4 mm. broad ; female spikes 2–5 mm. thick at maturity ; beak of utricle 0·2–0·75 mm. long, teeth 0·1–0·2 mm. long :

Female scales blackish-castaneous ; spikes approximate to sub-approximate, occupying the upper 3–5 cm. of the stem 18. *barbata*.

Female scales whitish, sometimes reddish-spotted ; spikes, except upper 2, more widely spaced, occupying almost the whole length of the stem .... 19. *Preissii*.

Stigmas 2 ; utricle more or less plano-convex, not trigonous :

Utricles whitish-hispidulous on the nerves above........ 7. *brunnea*.

Utricles glabrous, except on the margins above :

Spikes nodding, all peduncled, lower long-peduncled .. 26. *lobolepis*.

Spikes erect to suberect, all sessile or lower sometimes subsessile or shortly peduncled :

Terminal spike or spikes wholly male, remainder androgynaeceous to wholly female :

Leaves 4–9 mm. broad ; upper 1–3 spikes male, remainder about 5–12·5 cm. long ; utricles about 2·5 mm. long, obovate, nerveless or with very few obscure or slender nerves .... 28. *polyantha*.

Leaves 2–4 mm. broad ; uppermost spike male, remainder about 1·5–5·3 cm. long ; utricles 3–4 mm. long, ovate to elliptical, distinctly 4–6-nerved on each face.................. 29. *Gaudichaudiana*.

Terminal and all other spikes androgynaeceous :

Spikes very numerous, forming a slender contracted panicle 6–30 cm. long :

Utricles glabrous on the margins, beak glabrous or sparsely setulose .... 30. *declinata*.

Utricles setulose on the margins above, including the beak :

Stems triquetrous, solid ; female scales not or only very narrowly whitish on the margins above .... 31. *appressa*.

Stems terete, hollow ; female scales broadly whitish on the margins above .... 32. *tereticaulis*.

Spikes about 12, mainly compound and densely congested into a terminal, more or less oblong head 2·5–3·5 cm. long ; utricles many-nerved .... 33. *divisa*.

Spikes 6–8, all simple, forming a rather dense terminal, narrowly oblong to ellipsoid head 1·5–2·5 cm. long ; utricles nerveless .... 34. *chlorantha*.

Terminal spike gynaecandrous, others gynaecandrous or wholly female, but always wholly female in appearance :

Male part of terminal spike about equalling the female part ; scales blackish to blackish-red . 27. *hypandra*.

Male part of terminal spike shorter than the female part, usually much shorter, and so inconspicuous that the spike appears to be wholly female ; scales usually whitish or greenish-white, rarely more or less castaneous, never blackish-red :

Spikes ebracteate, rarely lowest spike with a subherbaceous bract up to as long as itself :

Utricles strongly reflexed at maturity, tapering beak broadly green-margined, about as long as the rest of the utricle, teeth about 0·25–0·5 mm. long .... 35. *echinata*.

Utricles patulous at maturity, tapering beak not marginate, much shorter than the rest of the utricle, teeth less than 0·1 mm. long .... 36. *curta*.

Spikes, or at least the lowest, with foliaceous bracts, the lowest of which exceeds and usually far exceeds the whole inflorescence :

Scales castaneous to spadiceous, at least in the upper part, with whitish margins :

Stems 25–40 cm. tall ; leaves about 1 mm. broad ; utricles 3 mm. long .... 37. ***Raleighii***.

Stems 4–20 cm. tall ; leaves 1–2 mm. broad ; utricles 3·5–4 mm. long ...... 38. *hebes*.

Scales whitish or greenish-white ; the scales of some Tasmanian plants of *C. inversa* are castaneous, but they lack a whitish margin :

Stems 1·5–2·5 cm. tall, not more than half as tall as the leaves .... 42.**paupera*.

Stems 4–100 cm. tall, usually taller than, and always more than half as tall as, the leaves :

Utricles not or scarcely transversely wrinkled at maturity .... 39. *inversa*.

Utricles conspicuously transversely wrinkled at maturity :

Utricles obovate to suborbicular, strongly transversely wrinkled, 6 or 7 times as long as the beak .... 39 *a*. *inversa* var. [*major*.

Utricles ovate-lanceolate, elliptical, or elliptic - lanceolate, extremely strongly transversely wrinkled, from about as long to 3 times as long as the beak :

Stems 40–100 cm. tall ; leaves 2–4 mm. broad ; spikes 8–15 mm. long and 5–10 mm. thick at maturity ; whole inflorescence 1·8–4·8 cm. long ; utricles 4·25–5 mm. long, beak about as long as the rest of the utricle ...... 40. *lophocarpa*.

Stems 15–45 cm. tall ; leaves 1–3 mm. broad ; spikes 4–7 mm. long and 3–5 mm. thick at maturity ; whole inflorescence 8–20 mm. long ; utricles about 3 mm. long, beak about one-third as long as the rest of the utricle .... 41.**rhytidocarpa*.

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* **Carex paupera** *Nelmes*, sp. nov. ; affinis *C. inversae* R. Br., sed planta tota minore, culmis 1·5–2·5 cm. altis sed dimidia folia haud superantibus, inflorescentia saepe pseudo-monostachya, praecipue differt. Type : *R. A. Black*. Mt. Hotham, Victoria.

* **Carex rhytidocarpa** *Nelmes*, sp. nov. ; affinis *C. lophocarpae* C. B. Clarke, sed planta tota minore, utriculi rostro circiter tertiam partem utriculi aequante, praecipue differt. Type : *Hubbard*. 5004. Wandoan, Queensland.

Enumeration.

The Australian distribution is indicated in the following list by the initial letters of the names of the States. H. stands for Lord Howe Island.

1. *Carex Rafflesiana* Boott in Trans. Linn. Soc. Lond. xx, p. 132 (1846); Kükenth. in Engl. Pflanzenreich, IV, xx, p. 282 (1909).—Q.

2. *C. Dietrichiae* Boeck. in Flora, LVIII, p. 122 (1875).—*C. fissilis* Boott, Benth. Fl. Austral. VII, p. 441 (1878).—*C. indica* var. *fissilis* Kükenth. p. 264, partim.—Q.

3. *C. Fleckeri* Nelmes in Kew Bull. 1939, p. 313.—Q.

4. *C. Hubbardii* Nelmes (*supra*, p. 279).—Q.

5. *C. longibrachiata* Boeck. in Linnaea, XLI, p. 282 (1877).—*C. longifolia* R. Br. Prodr. Fl. N. Holl. p. 242 (1810); Benth. p. 448; Kükenth. p. 650; *non* Tuckerm.—N.S.W., V.

6. *C. iynx* Nelmes (*supra*, p. 279).—V., T.

7. *C. brunnea* Thunb. Fl. Japon. p. 38 (1784); Kükenth. p. 599.—*C. gracilis* R. Br. p. 242; Benth. p. 442; *non* Curt.—Q., N.S.W.

8. *C. cryptostachys* Brongn. in Duperry, Voy. 'Coquille', Bot. p. 152, t. 25 (1828); Kükenth. p. 471.—Q.

9. *C. breviscapa* C. B. Clarke in Hook. f. Fl. Brit. Ind. VI, p. 736 (1894); Kükenth. p. 474.—Q.

10. *C. breviculmis* R. Br. Prodr. Fl. N. Holl. p. 242 (1810); Benth. p. 445; Kükenth. p. 469.—Q., N.S.W., V., T., S.A., H.

11. *C. Bichenoviana* Boott in Hook. f. Fl. Tasm. II, p. 101 (1860); Benth. p. 446.—*C. pumila* var. *Bichenoviana* (Boott) Kükenth. p. 740.—N.S.W., S.A., T.

12. *C. pumila* Thunb. Fl. Japon. p. 39 (1784); Benth. p. 445; Kükenth. p. 738.—*C. littorea* Labill. N. Holl. Pl. II, p. 69, t. 219 (1806).—Q., N.S.W., V., T., S.A., H.

13. *C. fascicularis* Soland. ex Boott in Hook. f. Fl. N.Z. I, p. 283 (1853).—*C. Pseudocyperus* Linn., Benth. p. 448.—*C. Pseudocyperus* var. *fascicularis* (Soland. ex Boott) Boott, Illustr. IV, p. 141 (1867); Kükenth. p. 696.—Q., N.S.W., V., T., S.A., W.A.

14. *C. alsophila* F. Muell. Fragm. VIII, p. 257 (1874); Benth. p. 447; Kükenth. p. 618.—V.

15. *C. conspicua* Boott ex C. B. Clarke in Kew Bull. Add. Ser. VIII, p. 82 (1908).—V.

16. *C. Gunniana* Boott in Trans. Linn. Soc. Lond. xx, p. 143 (1846); Benth. p. 446; Kükenth. p. 661.—N.S.W., V., T., S.A.

17. *C. Blakei* Nelmes in Kew Bull. 1939, p. 311.—N.S.W., V.

18. *C. barbata* Boott, Illustr. I, p. 68, t. 187 (1858).—*C. Gunniana* var. *barbata* (Boott) Kükenth. p. 663.—T.

19. *C. Preissii* Nees in Lehm. Pl. Preiss. II, p. 94 (1846); Benth. p. 446; Kükenth. p. 691.—*C. thecata* Boott in Trans. Linn. Soc. Lond. xx, p. 143 (1846).—W.A.

20. *C. tasmanica* Kükenth. in Bull. Herb. Boiss. sér. 2, IV, p. 59 (1904).—T.

21. *C. cataractae* R. Br. Prodr. Fl. N. Holl. p. 242 (1810).—*C. flava* Linn., Benth. p. 444.—*C. Oederi* var. *cataractae* (R. Br.) Kükenth. p. 675.—T.

22. *C. lacistoma* R. Br. Prodr. Fl. N. Holl. p. 243 (1810); Kükenth. p. 612.—N.S.W.

23. *C. Brownii* Tuckerm. Enum. Meth. p. 21 (1843); Benth. p. 447; Kükenth. p. 612.—*C. striata* R. Br. p. 243, *non* Michx.—N.S.W., V.

24. *C. canescens* Linn. Sp. Pl. ed. 1, p. 974 (1753).—*C. Buxbaumii* Wahlenb. in Vet.-Akad. Handl. Stockholm, XXIV, p. 163 (1803); Benth. p. 444; Kükenth. p. 393.—V.

25. *C. neurochlamys* F. Muell. Fragm. VIII, p. 258 (1874).—*C. maculata* Boott, Benth. p. 447.—*C. maculata* var. *neurochlamys* (F. Muell.) Kükenth. p. 428.—Q., N.S.W.

26. *C. lobolepis* F. Muell. Fragm. VIII, p. 258 (1874); Benth. p. 443.—*C. cernua* var. *lobolepis* (F. Muell.) Kükenth. p. 354.—N.S.W.

27. *C. hypandra* F. Muell. [Fragm. VIII, p. 259 (1874), *nom. provis.*] ex Benth. Fl. Austral. p. 439 (1878).—V.

28. *C. polyantha* F. Muell. in Trans. Phil. Soc. Vict. I, p. 110 (1855); Kükenth. p. 318.—*C. Cunninghamii* Boott, Illustr. IV, p. 171, t. 579 (1867).—*C. acuta* Linn., F. Muell. Fragm. VIII, p. 259 (1874); Benth. p. 443.—Q., N.S.W., V.

29. *C. Gaudichaudiana* Kunth, Enum. Pl. II, p. 417 (1837); Kükenth. p. 312.—*C. vulgaris* var. *Gaudichaudiana* (Kunth) Boott, Illustr. IV, p. 169, t. 567 (1867); Benth. p. 442.—*C. contracta* F. Muell. Fragm. VIII. p. 258 (1874); Benth. p. 442.—*C. Gaudichaudiana* var. *contracta* (F. Muell.) Kükenth. p. 313.—Q., N.S.W., V., T., S.A.

30. *C. declinata* Boott, Illustr. IV, p. 171, t. 580 (1867); Benth. p. 441; Kükenth. p. 171.—Q., N.S.W.

31. *C. appressa* R. Br. Prodr. Fl. N. Holl. p. 242 (1810); Kükenth. p. 178.—*C. paniculata* Linn., Benth. p. 440.—Q., N.S.W., V., T., S.A., W.A.

32. *C. tereticaulis* F. Muell. Fragm. VIII, p. 256 (1874); Benth. p. 441; Kükenth. p. 177.—N.S.W., V., T., S.A., W.A.

33. *C. divisa* Huds. Fl. Angl. ed. 1, p. 348 (1762); Kükenth. p. 125.—T.

34. *C. chlorantha* R. Br. Prodr. Fl. N. Holl. p. 242 (1810); Benth. p. 440; Kükenth. p. 141.—N.S.W., V., T.

35. *C. echinata* Murr. Prodr. Stirp. Gotting. p. 76 (1770); Benth. p. 439.—*C. stellulata* Gooden. in Trans. Linn. Soc. Lond. II, p. 144 (1794); Kükenth. p. 228.—V.

36. *C. curta* Gooden. in Trans. Linn. Soc. Lond. II, p. 145 (1794).—*C. canescens* Linn., Benth. p. 439; Kükenth. p. 216.—V., N.S.W.

37. *C. Raleighii* Nelmes in Kew Bull. 1939, p. 310.—V.

38. *C. hebes* Nelmes in Kew Bull. 1939, p. 310.—*C. hypandra* F. Muell., Kükenth. p. 190.—V.

39. *C. inversa* R. Br. Prodr. Fl. N. Holl. p. 242 (1810); Benth. p. 438; Kükenth. p. 189.—Q., N.S.W., V., T., S.A.

39*a*. *C. inversa* var. *major* Boott, Illustr. IV, p. 151, t. 486 (1867), partim.; Kükenth. p. 189, partim.—W.A., S.A.

40. *C. lophocarpa* C. B. Clarke in Kew Bull. Add. Ser. VIII, p. 69 (1908).—*C. inversa* var. *Leichardtii* Boeck. in Linnaea, XXXIX, p. 70 (1875); Kükenth. p. 189.—*C. inversa* var. *major* Benth. p. 438, *non* Boott.—Q., N.S.W.

41. *C. rhytidocarpa* Nelmes (*supra*, p. 282).—Q., N.S.W.

42. *C. paupera* Nelmes (*supra*, p. 282).—V.

43. *C. cephalotes* F. Muell. in Trans. Phil. Soc. Vict. I, p. 110 (1855); Benth. p. 437.—*C. pyrenaica* var. *cephalotes* (F. Muell.) Kükenth. p. 106.—N.S.W., V.

44. *C. Archeri* Boott in Hook. f. Fl. Tasm. II, p. 98, t. 150 (1860).—*C. acicularis* Boott, Benth. p. 437; Kükenth. p. 100.—V.

45. *C. capillacea* Boott, Illustr. I, p. 44, t. 110 (1858); Benth. p. 438.—*C. rara* subsp. *capillacea* (Boott) Kükenth. p. 102.—N.S.W.

PSEUDOSINDORA PALUSTRIS (LEGUMINOSAE, AMHERSTIEAE), A NEW GENUS AND SPECIES FROM BORNEO.

By C. F. Symington.

Pseudosindora *Symington.* Genus novum, inter *Crudiam* Schreb. et *Sindoram* Miq. medium, ab illa sepalis coriaceis, ovario glabro, seminibus arillatis, ab hac petalo absente, staminibus 10 subaequalibus perfectis, arillo magis carnoso semen amplectente praecipue differt.

Receptaculum brevissimum; calycis segments 4, subimbricata. *Petala* 0. *Stamina* perfecta 10, libera, subaequalia, leviter exserta; antherae oblongae, versatiles, longitudinaliter dehiscentes. *Ovarium* glabrum, 1–2-ovulatum, breviter stipitatum, stylo glabro incurvo, stigmate terminali subcapitato. *Legumen* rigide coriaceum, valvis 2 compressis (*Sindorae* ad instar); semina 1–2, oblonga, testa dura nitida, arillo carnoso semen amplectente.—Arbor magna: folia stipulata, imparipinnata, foliolis alternis coriaceis.

Species 1, e sylvis paludosis sublittoralibus Borneonis boreali-occidentalis tantum cognita.

Pseudosindora palustris *Symington* species nova adhuc unica. *Arbor* magna, glabra. *Ramuli* siccitate plerumque rubidi vel purpureo-brunnei. *Stipulae* auriculatae vel subfalcatae, mucronatae, membranaceae, usque circiter 1·5 cm. longae et 1 cm. latae, caducae. *Folia* 2–6 (plerumque 4–) foliolata, foliolis regulariter alternantibus; rhachis circiter 2–6 cm. longa, siccitate fusco-rubra; petiolus circiter 1·5 cm. longus, basi leviter incrassatus; foliola elliptico- vel ovato-oblonga, leviter inaequilateralia, apice breviter obtuse (interdum mucronate) acuminata, basi truncata vel rotundata, circiter 5–14 cm. longa et 3–8 cm. lata, nitida, coriacea, nervo marginali prominente, siccitate supra plerumque viridi-grisea vel purpureo-brunnea, subtus pallidius brunnea; costa supra leviter depressa, subtus argute carinata; nervi principales circiter 25-jugi, supra subtusque manifesti, subtiles tamen nec nervis intermediis re vera prominentiores; reticulationes subtiles sed plerumque utraque pagina manifestae; petioluli breves, robusti, circiter 5 mm. longi, siccitate fusci. *Paniculae* terminales vel axillares, plerumque foliis breviores (4–7 cm. longae); rhachis pilis aureis deciduis sparse vel dense induta; ramuli racemose dispositi, recti, usque 4 cm. longi, 3–8-flori, floribus spiraliter dispositis; bracteae bracteolaeque non visae, sed ut videtur parvae, cito caducae. *Pedicelli* aureo-pubescentes usque glabri, 2–4 mm. longi. *Calyx* maturus usque ad receptaculum divisus; lobi subaequales, alabastro leviter imbricati, maturi reflexi, circiter 5 mm.

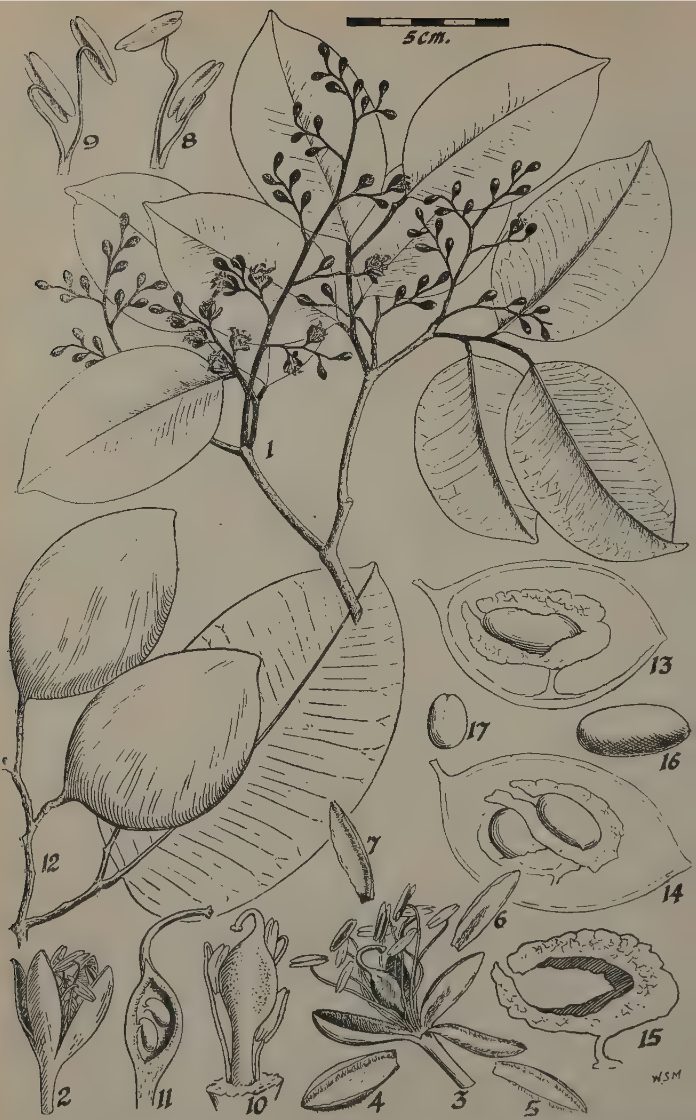

Fig. 1.—1, flowering branchlet; 2, flower bud, just opening; 3, mature flower; 4, 5, 6 and 7, sepals detached; 8 and 9, stamens; 10, ovary; 11, longitudinal section through ovary; 12, fruiting branchlet; 13 and 14, longitudinal sections through fruits, showing one and two seeds respectively; 15, aril removed from 13; 16, seed, lateral view; 17, the same, end view. (Drawings of 1 to 11 based on Forest Dept. F.M.S. 32600; 12 on 32577; 13 to 17 on 39501. (*Scale applies to 1 and 12–17 only.*

longi, oblongo-lanceolati, extra glabrescentes, intus (margine glabro excepto) dense tomentosi. *Stamina* subaequalia. matura calycem leviter superantia; filamenta filiformia; antherae oblongae, circiter 2 mm. longae. *Ovarium* breviter stipitatum, glabrum vel pilis paucis longis aureis instructum, pauciovulatum; stylus ovario subaequilongus, recurvus, glaber; stigma parvum, capitatum. *Legumen* breviter stipitatum, ellipticum, utrinque acutum, circiter 4·5–6 cm. longum, maturum circiter 1·5 cm. crassum, glabrum; semina 1 vel 2, oblonga, leviter dorsaliter sulcata; testa lignosa, viva nitide fusco-brunnea usque nigra; funiculus albus, circiter 5 mm. longus; arillus roseus, cristam gallinaceam revocans, semen omnino amplectens.

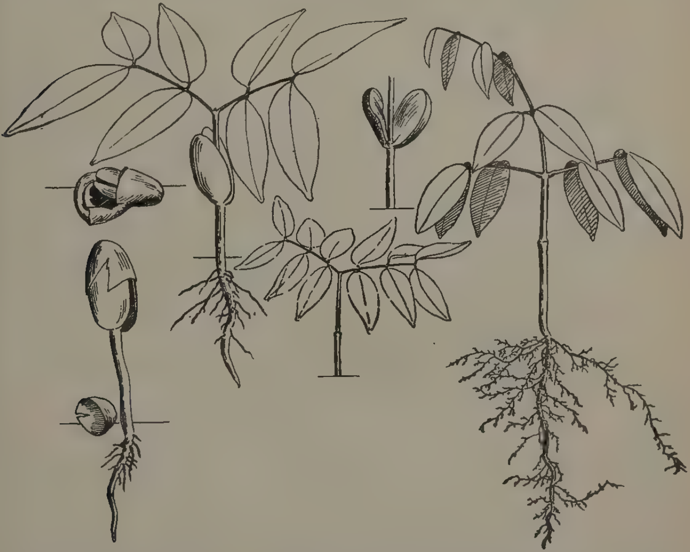

FIG. 2.—Various stages in the germination of seed of *Pseudosindora palustris* Sym.

SARAWAK. Sine loc., 1865–8, flower, *Beccari* 3915 (Herb. Kew.); 1922, *D. Carroll* (For. Dep. F.M.S. 7171).

BRUNEI. Anduki state land, flat sandy soil, semi-swamp, flower 4 April, 1938, *C. O. Flemmich* (For. Dep. F.M.S. 32600; *typus*, Herb. Kepong): 'Tree, 90 ft. high, 69 in. girth; flower pearl-fawn-coloured.' Also For. Dep. F.M.S. 28679, 32577, 35703, 35723, 36979, 37188, 37189, 39501.

This interesting species is one of the common and distinctive trees of the coastal fresh-water swamp-forests of Brunei. It occurs also in Sarawak, where it was collected in flower by Beccari (*Becc.* 3915), and it is surprising that it has escaped botanical recognition for so long. In addition to the sheet of Beccari's collection preserved at Kew, I have

only seen the one made by D. Carroll in Sarawak in 1922, and those of members of the Malayan Forest Service in Brunei since 1932.

The tree is well known to the natives in Brunei by the name *sĕpĕtir*, *sepĕtir paya*, or some variant of these names. The name *sĕpĕtir* is commonly applied to species of *Sindora*, both in Brunei and in the Malay Peninsula. *Pseudosindora palustris* certainly resembles species of *Sindora* in leaf and fruit characters, but there are many very distinctive field characters. For example, the bark is minutely fissured, whereas in *Sindora* it is smooth. The pods resemble those of some smooth-fruited species of *Sindora*, but the seed has a large, fleshy aril encircling it: in *Sindora* there is a thick horny, obconic, arillate funiculus. The germination of the seed is similar to *Sindora*, but the first pair of true leaves are opposite: in *Sindora* all leaves are alternate. The wood-anatomical structure is similar to *Sindora*, but there are no intercellular canals.

Pseudosindora palustris is a tall unbuttressed tree reaching a diameter of about 6 ft. at breast height. The timber is neither durable nor decorative and the only recorded use is for the masts of boats, for which purpose small trees are selected. Nevertheless, its moderate hardness, and the good shape and local abundance of the trees, suggest that it may some time be employed in plywood manufacture.

The genus *Sindora* (or *Echinocalyx* Benth.) was placed by Bentham and Hooker (Gen. Pl. I, p. 461; 1865) and Taubert (in Engl. u. Prantl. Pflanzenf. III, p. 132; 1892) in the tribe *Cynometreae*, but is clearly most closely related to *Pahudia*, *Afzelia* and other genera of the tribe *Amherstieae*, in which it was placed by King (in Journ. As. Soc. Beng. LXVI, pt. 2, p. 202; 1897).

A NEW SPECIES OF RAPANEA (MYRSINACEAE) FROM LORD HOWE ISLAND.

By T. A. SPRAGUE, D.Sc., F.L.S.

The tropical and sub-tropical genus *Rapanea* now includes over 200 described species. It is well represented in Australasia and the Pacific Islands, and two species have been recorded from Lord Howe Island, namely, *R. myrtillina* Mez and *R. platystigma* (F. Muell.) Mez (Myrsinaceae in Das Pflanzenreich, IV, 236, p. 370; 1902). To these is now added a third, collected in 1937, 1938 and 1941 by Capt. J. D. McComish, who has increased greatly our knowledge of the floras of Lord Howe Island and Norfolk Island.

The substance of Capt. McComish's observations on the new species is here reproduced.

> No. 159. During my recent visit [1938] I saw several of these trees. Trees 40–50 ft. high, 8½ in. or more in diameter at breast height. Bark greenish-brown, irregularly blotched with grey, 5/16 in. thick, tissue reddish-brown. Leaves crowded towards the ends of the branchlets, up to 2⅞ in. long by 1 in. wide, margins inclined to turn downwards; midrib much lighter in colour than the blade, prominently raised below, slightly above. Young leaves rather densely covered with purple spots which could not be seen on the old leaves. Fruit a drupe, purple when ripe, more or less rounded, about ¼ in. in diameter, usually solitary, but sometimes in twos or threes; stalk 3/16 in. long. A young tree, 25 ft. high, 3 in. in diameter at the ground, bore leaves up to 5¾ in. long by 2¼ in. wide.

Other specimens of *Rapanea* from Lord Howe Island sent to Kew by Capt. McComish are Nos. 70, 70A, 70B, 70C (all *R. platystigma*), and No. 70D (*R. myrtillina*). He supplied the following comparison between No. 70 and No. 159 :—

Size.—Most trees of No. 70 do not exceed 20 ft. in height, whereas many of No. 159 reach a height of 50 ft.

Manner of growth.—Branches and branchlets of No. 70 are inclined to be angular, close together, making a fairly dense head, whereas those of No. 159 are more or less curved, not close together, giving a more open and spreading head.

Leaves.—The leaves of No. 70 are smaller than those of No. 159 and vary greatly in size and shape. Those of No. 159 are fairly uniform in size and shape.

Fruit.—The fruit of No. 70 is smaller than that of No. 159, and the fruiting is much more profuse.

The new species is appropriately named after its discoverer, and the following technical description is supplied :—

Rapanea McComishii Sprague, sp. nov. ; affinis *R. platystigmati* (F. Muell.) Mez, a qua ramulis laxe dispositis crassioribus, foliis majoribus subtus minute dense punctatis, fructibus majoribus differt.

Arbor glabra, 12–15 m. alta, 21 cm. diametro 1·2 m. supra basin. *Rami* 4–5 mm. diametro 10–15 cm. infra apices, in sicco corrugati ; ramuli laxe dispositi, leviter curvati, circiter 2 mm. diametro. *Folia* versus apices ramulorum congesta ; lamina oblongo-oblanceolata, apice rotundata, subtruncata vel leviter retusa, in petiolum sensim angustata, 3·5–6·5 cm. longa, 1·3–2·4 cm. lata (folia ramulorum sterilium arboris juvenis 5–14 cm. longa, 2·5–5·5 cm. lata, petiolis usque 1 cm. longis), supra minute dense crassiuscule reticulata inconspicue punctata, subtus laevia densissime fusco-punctata punctis circulis pallidioribus cinctis, margine cartilaginea leviter recurva, costa pallidiore supra laminam infra ejus medium leviter prominente apicem versus impressa infra laminam valde prominente ; petioli 4–6 mm. longi, leviter marginati, in sicco minute transverse lineato-corrugati. *Umbellae* in axillis foliorum exstantium et delapsorum ortae, 4–6-florae ; pedunculi crassi, 2 mm. longi ; bracteae ovato-cupulares ; pedicelli in foveis bractearum inserti, 1·5–2 mm. longi. *Flores* pentameri, ut videtur hermaphroditi. *Calyx* cupularis ; tubus 0·3–0·4 mm. longus, sparse glanduloso-punctatus ; lobi ovato-triangulares, obtusi vel rotundati, vix 1 mm. longi, sparse glanduloso-punctati, vel glanduloso-lineati lineis 2 longitudinalibus, margine glabri. *Corollae tubus* 0·75 mm. longus, pauciglanduloso-punctatus ; lobi patuli, ovato-oblongi, obtusi, 1·75 mm. longi, brunneo-punctati et lineati, minute dense papillato-ciliati. *Antherae* basibus corollae loborum affixae, ovato-oblongae, superne incurvae, apice anguste rotundatae, 1 mm. longae. *Ovarium* ellipsoideo-globosum, 1·5 mm. diametro ; stigma brunneum, carnosum, pulvinatum, irregulariter angulatum vel lobatum, circiter 1 mm. diametro ; ovula 4. *Drupa* globosa, 6 mm. diametro, purpurea, pedicello 3 mm. longo suffulta.

LORD HOWE ISLAND.—Capt. McComish, No. 159 :—fruiting material collected in Feb. 1937 and Nov. 1938 ; and flowering material collected in July 1941 (typus in Herb. Kew.).

Among the most obvious characters separating *R. McComishii* from *R. platystigma* are the much laxer branching, stouter branchlets, fewer umbels, and the shorter time during which the old peduncles persist after the fall of the fruits. The branches and branchlets of *R. platystigma* are conspicuously verrucose, owing to the long persistence of the peduncles, which is not the case with *R. McComishii*.

OBITUARIES.

Edgar Johnson Allen was born at Preston in 1866. He died on 7 December 1942. His biological work covers a period of fifty years, during almost the whole of which time he was Director of the Marine Biological Laboratory at Plymouth. Few zoologists have had an influence over so long a time. Few have gone about their work with such unassuming kindness and effectiveness or have endeared themselves to biologists of such different ages and outlooks. No one who knew Allen could fail to be impressed with the width and intensity of his interest in biology.

Allen's wide outlook began with his training. He started his career in the physical sciences. Graduating as an external student of London University, he took honours in chemistry in the intermediate B.Sc. (1884), and physics in the final examination (1885). It was not until later that he turned to biology after a short period of teaching, first as science master at Dunheved College, Launceston, and then as headmaster of Coke College, Antigua. But he soon returned from the West Indies, to work for a year under F. E. Schulze in Berlin. After this he did research for a time under Weldon at University College, London, and in 1892 he spent ten weeks at Plymouth, occupying the British Association Table for part of the time. Thus began his long association with Plymouth.

At that time conditions at the laboratory were rather difficult. The first flush of enthusiasm following its opening in 1888 had passed by. Funds were not great, and there had been a rather rapid series of changes in the directorship. In 1895 Allen was appointed Director of the Laboratory and Secretary to the Council. He held these posts till 1936, when he retired after 42 years' work. No better choice could possibly have been made by the Council for their new Director.

Allen's earlier work was concerned with the structure of the excretory organs and nervous system of the decapod Crustacea, and throughout his career he turned occasionally to problems of pure zoology. He published some valuable papers on the Polychaeta, a group in which he was especially interested. But on becoming Director of the Laboratory, he immediately took up work which was essential for its future During the next ten or fifteen years he published by himself and with his staff a series of papers on the fauna of the Plymouth region. In addition, he undertook work both with a direct bearing on fishery problems and on the fundamental scientific questions on which these are based. It is interesting to look back at his early papers on mackere and sunshine (1909) and on the artificial culture of marine diatoms

(1910, 1914), and to think how greatly such early work has borne fruit in the fishery and oceanographic investigations done at the present day, not only at Plymouth but elsewhere in the world as well.

Allen was interested in life in the sea in all its aspects. He saw the importance both of the direct attack on the practical problems of the fisherman and of free 'academic' research on the fundamental questions involved in these. His interest in fisheries was much more than a local one. In his early days he reported on the sponge fishery of Florida and the artificial culture of sponges. He was of international repute in European fishery matters and was deeply interested in the work of the International Council for the Exploration of the Sea from its beginning. In 1902 the Marine Biological Association was asked by the Treasury to undertake the English scientific investigations connected with the Council's programme on the natural history of marketable marine fishes. This, presently, led to the foundation of an auxiliary laboratory at Lowestoft, to which was attached a steam trawler, the 'Huxley', and to work which remained with the Association until the laboratory was taken over by the Ministry of Agriculture and Fisheries in 1910. The separation of some of the work directly concerned with the fishing industry enabled Allen to turn the Plymouth laboratory towards those fundamental problems which now appeared to lie behind the immediate practical ones, particularly towards an understanding of the biology and chemistry of sea water. Allen was remarkably skilful in the way he directed the work. Unguided 'academic' research in biology may lead rather far afield, so that while results ultimately of great value are obtained, the immediate solution of urgent practical needs may not be achieved. On the other hand, few things are more deadly over a long period than the confinement of scientific activity to the attempted direct solution of a practical problem. Too often the problem under these circumstances becomes elusive, and years of work may produce little result. Allen knew how to leave his colleagues unfettered in their work, while at the same time he would skilfully guide them by suggestion towards those goals; the importance of which he foresaw in both pure and applied biology.

Allen was able to do these things because of the grand view which he had of biology as a whole. He was no mere biologist with a benevolent attitude towards activities outside his subject. Partly by nature and partly because of his physical upbringing, he saw biological phenomena in their place in the whole sphere of science. It was this that enabled him to see what the work of a marine station should be, and during the last fifteen years of his directorship it enabled him to make the Plymouth laboratory one of the foremost marine stations of the world. By attracting visiting workers in all biological fields and also those who were interested in the physics and chemistry of the sea, he performed an invaluable service to biology. But it was not only his wish to see such work done by visitors: he was sure of the value of the repercussion of such work on those engaged on long-term problems in the staff of the laboratory. To make the most of these advantages is difficult, for there must inevitably be some clash of interests at a laboratory where some are employed continuously on long-term problems while others arrive in numbers from universities to work for brief periods i the year. But, under Allen's happy guidance, all went smoothly and al were refreshed by interchange of ideas.

Allen's wide outlook and his kind nature helped British biology i another way. After the last war, there was, for a short time, som misunderstanding between some of the older zoologists who identifie the field of zoology too rigidly with that of pure morphology, and som of the younger workers who began to attack experimental problems Allen's influence on those who worked at Plymouth was great in showin the unreality of dividing lines in zoology. His encouragement and advice particularly to young people, did much to set British zoology on th right road.

Allen was always interested in fundamental biological questions particularly those concerned with heredity and evolution. He inspire some interesting genetic work on *Gammarus*, and from time to tim gave his views on such subjects. His Hooker lecture on the Origin o Adaptations is of great interest. It was delivered in 1929, the year tha he was elected Fellow of the Linnean Society.

Allen's work brought him honour; perhaps a less disinterested ma would have received even more for the work he did, for he was alway content to see the goal for which he worked achieved by others. H took his D.Sc. (London) in 1900. He was elected Fellow of the Roya Society in 1914, and in 1922 he was President of the Zoological Sectio of the British Association. The Hansen Memorial Medal and Priz was given to him from Denmark in 1923 in recognition of his work i marine microbiology.

On 24 May 1926 he received the Linnean Medal. The year he retired 1936, he was awarded the Darwin Medal of the Royal Society. Th U.S. National Academy of Sciences, Washington, gave him the Agassi Medal for oceanography (1938), and he was made a Fellow of Universit College, London, in the same year. He was a foreign member of th Royal Academy of Denmark and an Hon. LL.D. of the University o Edinburgh. His great public service to fisheries received a recognitio in the award of the C.B.E. in 1935. When he retired, he was mad an honorary Governor of the M.B.A., an honour not previously conferred on anyone.

He took an active interest in local affairs, both in Plymouth and i the County. He was at one time President both of the Plymout Institution and of the Devonshire Association.

Allen did great work. Without it, British biology would have bee the poorer. But, perhaps, of all his characteristics that which stand out the most was his kindness to young people. Though naturally shy man, he was never so with children. He was at his happiest i their company and they understood each other. And great was hi kindness and helpfulness to the young research worker. There wer many who worked at Plymouth during the period between the two war who will remember his knock on the door while they worked there in th evening, and they will remember his interest in what they were doin his pleasant conversation and his helpful advice.

C. F. A. Pantin.

Surgeon Rear-Admiral Walter Godfrey Axford, C.B., R.N., M.R.C.S., L.R.C.P., died at the age of 81 at King Edward VII Hospital, Windsor, on 23 February 1943.

He was trained at Westminster Hospital, qualifying from Edinburgh. He joined the Navy and was first posted to the North American Station, visiting the West Indies, etc., in H.M.S. 'Comus', one of the old 'wooden walls'. He was then appointed to the R.N. Hospital at Bermuda, where he married. Afterwards he was stationed for two years on Ascension Island. Later he was for nearly four years on the Australian Station, in H.M.S. 'Pylades'. He served in many naval hospitals in Great Britain, on the Island of Haulbowline in Cork Harbour, and also with the Mediterranean Fleet. From 1914–1916 he worked on the surgical side of the R.N. Hospital, Chatham, and from 1916–1918 he was in charge of the surgical section of the R.N. Hospital, Haslar: for this work he was awarded the C.B. in 1919. After his retirement, Rear-Admiral Axford interested himself in the work of treating the men who were suffering mentally from the effects of the Great War.

He was a very keen and capable field botanist and had many friends among members of both The London and The Haslemere Natural History Societies, in which he was particularly active. He was elected to the Fellowship of the Linnean Society in 1893. G. R. A. Short.

Albert William Bartlett, who died on 4 March 1943 at the age of 68, became a Fellow of the Society as far back as 1903. Although by profession a botanist, he was known to confess to a preference for zoology, and his attitude towards biology was essentially the broad one of the naturalist.

His early education was at Hurstpierpoint College, from which he passed to university studies, first at Aberystwyth and then at the Royal College of Science, London.

In 1896 he was appointed Science Master at the Secondary School, Henley, but found school teaching little to his liking and in 1899 he returned to college, this time to Cambridge, where he took a First Class in Botany in Part II of the Natural Science Tripos.

A fruitful period of work followed as Superintendent of the Botanic Gardens, Georgetown, British Guiana, where his work included editing the Journal of the Board of Agriculture of British Guiana.

He returned to England in 1909 and became assistant in the Botany Department of Sheffield University, where he remained till 1920, interrupted by a period in the Army from 1914–1919. This was spent, for the most part, as a private in the R.A.M.C. in Gallipoli and Palestine.

In 1920 he was appointed Lecturer in Botany at Armstrong (now King's) College, University of Durham, at Newcastle-upon-Tyne, and continued to teach there until 1939, when he had a stroke, from the results of which he never completely recovered.

In Newcastle he took a very keen interest in the natural history activities of the city and district: he served long periods on the councils and took high office in the Northumberland and Durham Natural History Society, the Wallis Club and the Northern Naturalists' Union. He was also for some years a member of the editorial board of 'The Vasculum' and, though he was not a frequent contributor, his articles were so clearly and simply written that they were greatly appreciated by amateurs and professionals alike. Both here and in the scientific journals, he wrote chiefly on the Fungi. His paper on the new species *Urophlyctis Potteri* ('On a new species of *Urophlyctis* producing Galls on *Lotus corniculatus* Linn.', Trans. Brit. Mycol. Soc. XI, pts. iii & iv, Dec. 1926) is probably his most important contribution to scientific literature. He has enriched the local archives by keeping a card index of fungal records for Northumberland and Durham, from which new vice-county records were published from time to time in 'The Vasculum'.

As a lecturer he was noted for the great care which he took in preparing both lectures and laboratory classes, and for the neatness and orderliness which pervaded everything he did.

By nature he was shy and retiring, yet that never held him back from kindly actions, and he was generous to a fault.

K. B. BLACKBURN.

SIR EDWIN JOHN BUTLER, C.M.G., C.I.E., M.B., F.R.S.—Edwin John Butler was born on 13 August 1874 in County Clare, Eire. He died suddenly on 4 April 1943 at Esher, Surrey, following an attack of influenza.

He was educated at Queen's College, Cork, where he became senior scholar in 1896, and then studied medicine and in 1898 took the M.B. (Hons.) at the Royal University, Ireland. He never practised, as his interests lay in other directions. During 1899 and 1900 he held a travelling scholarship and studied botany at Paris, Freiburg, Antibes and Kew. He showed an early interest in mycological problems and paid particular attention to the genus *Pythium* and other fungi associated with the soil.

The beginning of the present century saw the first stirring of interest in scientific research in agriculture by the Government of India, resulting in the appointment of specialists in various sciences, and thereby throwing open an immense field for investigational work. Butler applied for and was appointed to the post of cryptogamic botanist to the Government of India—the first of its kind in that country—and arrived in Calcutta in 1901, being transferred to Dehra Dun in 1902. In the meantime a decision had been made to establish an Imperial Department of Agriculture for India and to build the necessary laboratories and buildings at Pusa in Bihar.

In 1905 he was transferred to Pusa as Imperial Mycologist at this new Agricultural Research Institute and commenced the work which established his great reputation as a scientific investigator. He stayed at Pusa until 1920, becoming joint-director in 1919 and Agricultural Advisor to the Government of India in the following year. He only held this position for a short time, however, for towards the end of 1920 he returned to England as Director of the newly formed Imperial Bureau of Mycology. The success of this Institute was largely due to his personality and wide knowledge and his advice was in constant demand.

In 1935 he left the Imperial Mycological Institute and became Secretary to the Agricultural Research Council. Failing health led to his resignation in 1941, but he still maintained his interest in scientific developments and continued to sit on such bodies as the Colonial Advisory Council of Agriculture and the Scientific Committee of the Empire Cotton Growing Corporation, where his wise counsel and wide knowledge were in constant demand.

At the time of his death he was engaged on the production of a new revision of his work 'Fungi and Disease in Plants'. This book had been first published in 1918 and embodied much of the work in which he had been engaged during his seventeen years in India. He rounded off his Indian work by publishing, in 1932, 'The Fungi of India' conjointly with G. R. Bisby. This work is a compilation of the species recorded up to 1930 and their literature. Butler published many monographs and papers during his service in India and is always regarded as the 'father' of mycology in that country. Among his special publications may be mentioned the monographs on sugar cane diseases, wheat rusts, Fusarum wilts, and rice diseases, and five papers on the micro-fungi in conjunction with H. & P. Sydow, based on his own collections and containing many new records.

One of the most striking features was his attitude towards plant diseases. As a member of the research staff of an Agricultural Institute he realized that it was not sufficient merely to identify a disease but that it was necessary to investigate it from a critical point of view with the object of securing means of prevention or mitigation to the crops affected. He always insisted on detailed investigation in the field and, in fact, often emphasized the point that, in many cases, the incidence of a disease may be caused by faulty measures of cultivation or soil conditions. This led him to acquire an intimate knowledge of agricultural methods and conditions in many parts of India, and his powers of deduction were such that one came to value his advice and judgment on problems which were, strictly speaking, more agricultural than mycological. For example, when called to advise on the 'bud rot' disease of coco-nuts, which, some thirty years ago, was decimating the groves of the Madras Presidency, the treatment advocated was definitely practical and was concerned with the agricultural system then in practice.

Apart from his high scientific attainments Butler was a good organizer, and this was proved by the manner in which he initiated the Mycological Bureau at Kew and the way in which he organized the first Imperial Mycological Conference in 1924, and for many years edited the 'Review of Applied Mycology'. In 1926 he was elected F.R.S. and attended the International Congress of Plant Sciences at Ithaca as Chairman of the Mycological Section.

His services were on several occasions sought, in order to unravel problems concerning plant diseases of the greatest economic importance to the Empire. Thus, in 1927, he was invited to inspect the tea plantations in Nyasaland which were being attacked by a mysterious disease—'tea yellows'. The solution, worked out with R. Leach, has proved successful. Again, in 1931 he was called to the Sudan, where 200,000 acres of irrigated cotton were threatened by the 'black arm' disease. He received many honours. His service in India earned the C.I.E., and his work afterwards for the Empire as a whole, the C.M.G. in 1932. His knighthood came in 1939. For many years he was a Fellow of the Linnean Society of London and in 1929 was Vice-President.

His personality endeared him to everybody. He was invariably calm and unruffled and his tact and delicate sense of humour helped to get over many of the difficulties that are apt to arise when debates at conferences or committees tend to become acrimonious or too personal. He was a clear thinker and possessed an analytical brain, so that his judgment was universally respected. His loss will be greatly felt not only by his friends but also by the many who have read his works but never had the opportunity of meeting him in person.

He is survived by Lady Butler and by a son and two daughters.

G. Evans.

Herbert Edward Forrest (1858–1942), who died at his home, Hillside, Bayston Hill, Shrewsbury, on 6 November 1942, at the age of 84, was distinguished both as a naturalist and as an antiquary. Born at Wolverhampton on 18 May 1858, he was educated at Shrewsbury School, and afterwards entered Lloyds Bank, but after seven years as a bank clerk joined his brother in carrying on the pianoforte and music business which had been established in Shrewsbury by their father. Of this business, Mr. Forrest became the sole proprietor in 1919.

Natural history made a strong appeal to Mr. Forrest from his earliest days. While a bank clerk at Birmingham, he took up the study of pond life, and his first paper, published in the 'Midland Naturalist' in 1879, was on the Vorticellidae. In 1878 he became joint honorary secretary of the Birmingham Natural History Society, and a year or two later was elected a Fellow of the Royal Microscopical Society.

In 1893 the Caradoc Field Club and the Severn Valley Field Club, two old-established Shropshire naturalists' societies, amalgamated as the Caradoc and Severn Valley Field Club. Mr. Forrest became honorary secretary of the Club—an office which he held until 1929, when he relinquished it to become president. The latter position he still occupied at the time of his death. For nearly fifty years Mr. Forrest was the chief inspirer and leader of the club's varied activities. He played a leading part in organizing its meetings and excursions; he contributed numerous papers, lectures and talks to its proceedings; he frequently acted as leader of its excursions and field meetings; while as referee for zoology he co-ordinated the observations of its members and made the annual 'Record of Facts' a valuable repository of information concerning the natural history of Shropshire and North Wales.

In his first independent publication, Mr. Forrest demonstrated one of his most notable characteristics—his all-roundness. All over the country people were producing volumes on 'The Birds of ——', but in 'The Fauna of Shropshire' (1899) he boldly tackled the mammals, reptiles, batrachians and fishes as well, and even treated these groups with a greater fullness than he accorded the birds. Though designed on slighter lines than many county faunas, and now in many respects out of date, this volume was a creditable achievement for its time, and adequately filled a hiatus in the literature of the county.

For the next seven years Mr. Forrest was busily engaged on what was, perhaps, his most important work in the field of natural history. This was 'The Vertebrate Fauna of North Wales', a substantial volume of over 600 pages, which was published in 1907. The collection and collation of the material for this book involved a tremendous amount of work. Although its attractions for the naturalist had not been overlooked, North Wales had not hitherto attracted systematic notice, and Mr. Forrest had to break a good deal of fresh ground in attempting to determine the distribution of various species. He travelled widely to make his own observations, and carried on an extensive correspondence with other naturalists in all parts of the area. The result was a volume which for the first time did justice to a region of unusual interest and richness from the naturalist's point of view, and one which still holds its place as a standard work, although it inevitably now requires revision in some respects. Mr. Forrest always retained his interest in North Wales, and twelve years later produced a 'Handbook to the Vertebrate Fauna of North Wales' (1919), which recorded a good deal of information supplementing that contained in the earlier volume.

In the 'Victoria County History of Shropshire' (1908) the articles on vertebrate zoology were all contributed by Mr. Forrest. In addition, he wrote many papers and notes for such periodicals as 'The Zoologist', 'The Naturalist', 'British Birds' and 'The North-Western Naturalist', and for many years conducted a 'Nature Notes' feature in the 'Shrewsbury Chronicle'. In 1899, in association with R. A. Buddicom, he reorganized the Shrewsbury Natural History Museum, and afterwards became the honorary curator of zoology. He also undertook the rearrangement of the museums at Welshpool and Whitchurch (Salop), and arranged and catalogued the extensive Hawkstone collection of British birds. He was elected a Fellow of the Linnean Society in 1930.

As an antiquary, Mr. Forrest devoted special attention to the hitherto rather neglected subject of old houses, and produced a notable series of publications in which he correlated the architectural study of the houses themselves with the stories of the families which lived in them. 'The Old Houses of Shrewsbury'—his most popular book in this field—was published in 1911, and several later editions have been called for. 'The Old Houses of Wenlock and Wenlock Edge' came out in 1915, and 'The Old Houses of Stratford-on-Avon' was published in 1925. These books were supplemented by a series of papers on 'Some old Shropshire houses and their owners', which appeared in the 'Transactions' of the Shropshire Archaeological Society.

Among Mr. Forrest's other historical publications were 'The Old Churches of Shrewsbury' (1922), 'Shropshire in English History' (1923), a privately-printed 'History of the Forrest Family of Birmingham and Shrewsbury' (1923), and the 'Shrewsbury Burgess Roll' (1924), which he abstracted and edited for the Corporation of Shrewsbury and the Shropshire Parish Register Society. He also wrote short accounts of Shrewsbury and Stokesay Castles, and numerous papers for the Transactions of the Shropshire Archaeological Society. For some thirty years he edited the 'Shropshire Notes and Queries' column in the 'Shrewsbury Chronicle'. He was engaged by Sir Charles Phillipps Wolley to superintend the reconstruction of Old Parr's Cottage at Middletown, and wrote an account of the house and its famous occupant of 350 years ago. He had been a member of the council of the Shropshire Archaeological

Society since 1914, and secretary of the Shropshire Historical Antiquities Association since 1921.

For his services to local history and natural history, Mr. Forrest was made an honorary freeman of Shrewsbury in 1938.

During the last years of his life Mr. Forrest's energies were largely directed to the promulgation and advocacy of his theory of the origin and cause of the Ice Age, first announced in his presidential address to the Caradoc and Severn Valley Field Club in 1930, and fully expounded in his book, 'The Atlantean Continent', three years later. A revised edition was published in 1935. Founded to a great extent on zoological considerations, Mr. Forrest's theory has so far failed to win general acceptance among geologists. This was a disappointment to him, but he was undaunted in his defence of a theory which he believed to represent his most important work. Only a day or two before his death he was busily working on a new point which had occurred to him and which he hoped to put before the Linnean Society in the form of a paper.

Vigour of mind and body was a notable characteristic of Mr. Forrest; right up to the last he retained the zest and eagerness of a man less than half his age. Only bad weather prevented him from briskly walking the four miles from home to business each morning—a journey which he made within a week of his death—and he was always at business by 9 a.m. On field club excursions he was always in the forefront, undeterred by the steepest hill or the roughest path, and ever ready to turn aside to inspect some 'find' or to solve some problem which had presented itself. Remarkable catholicity of interests, quickness of perception and resilience of mind were notable features of his personality, and with them went an ever-ready willingness to put his knowledge and experience at the service of other students. L. C. Lloyd.

In the passing of Miss Alice M. Geldart on 4 May 1942, at the age of 80 years, Norwich lost a striking personality. Her father, H. D. Geldart, a Norwich wine merchant, was a well-known Norfolk phanerogamic botanist, and his daughter followed him as a worthy successor; his herbarium, with additions by Miss Geldart, has been given to the Norwich Castle Museum.

My first remembrance of her, many years ago, was when she was superintendent of the Sunday School of St. Matthew's, Thorpe Hamlet, a Norwich parish where, for the whole of her adult life, she took a prominent part in religious and social work..

One of her earliest and most cherished botanical recollections was when the British Association visited Norwich in 1868, and as a little girl she sat upon the knee of the Rev. M. J. Berkeley during his stay at her father's house. During her father's long life she met most of the working botanists resident or making excursions into Norfolk:—Hampden Glasspole, Arthur Bennett, Rev. E. F. Linton, Col. Feilden, Thomas Kitton, Clement Reid and Thomas Brightwell. It was fitting that during the return visit of the British Association in 1935 that she should take a responsible part, being local secretary of the Botany and Forestry Section. In the arranging of botanical excursions her thorough attention to detail brought high praise from those who enjoyed the visits to the heaths and broads of the county.

In her later years Miss Geldart took an active part in the proceedings of the Norfolk and Norwich Naturalists' Society and was twice its President. In 1914 her presidential address was 'Sir James Edward Smith and some of his Friends', and when, in 1931, she again filled the office, she took as her subject 'The Hookers in Norfolk and Suffolk'. She also contributed a paper upon *Stratiotes aloides* Linn. to the Transactions, of which she was for a time editor. Her work in the field of botany was recognized by her being admitted a Fellow of the Linnean Society and Hon. Member of the Norfolk and Norwich Naturalists' Society.

Miss Geldart possessed a fine botanical library and paid frequent visits to Aberdeenshire, the Hebrides, the Channel Islands, Devon and Switzerland in pursuit of her studies, and was for many years a member of the British Botanical Society and Exchange Club.

Always a strenuous worker, her other interests were: Egyptology (secretary of the local Egyptian Society for many years), music (violinist in the Norwich Philharmonic Society), chess, gardening, leather, metal and woodwork, water-colour painting, and she was president of the Norfolk and Norwich Library. H. J. HOWARD.

GEOFFREY THOMAS, fourth MARQUESS OF HEADFORT, died suddenly at Cahir Park, County Tipperary, where he was the guest of Col. Charteris, on 29 January 1943.

Born in June 1878, he was the second son of the third Marquess by his second wife, Emily, daughter of Lord John Thynne. He succeeded his father at the age of sixteen. Lord Headfort was educated at Mortimer School, Berkshire, and Harrow. As a young man he joined the Life Guards. In the war of 1914–18 he served in Gallipoli, Salonika and France. He was mentioned in despatches and retired as a Captain. He was a member of the first Irish Senate.

He was, perhaps, best known as an arboriculturist and horticulturist. He was president for many years of the Royal Horticultural and Arboricultural Society of Ireland, and was a vice-president of the Royal Horticultural Society. He became well known in the arboricultural world for the remarkable collection of Conifers that he formed on his estate at Kells, County Meath. Beginning in 1912, he formed a 'pinetum' of some 12 acres in extent, choosing for the site an island in a part of the park where the River Blackwater broadens out. He planted specimens of every available conifer, and as the rainfall is heavy, the soil very good, and the climate mild, the trees have flourished. On few estates in Great Britain is there such a representative collection of spruce trees. At the Conference on Conifers held at Vincent Square in 1931, Lord Headfort's exhibit of living Conifers, branches and cones from his estate was so complete and meritorious that it gained the Veitch Memorial Medal. He had a critical knowledge of the Coniferae, and a most retentive memory for plants. His collection of Rhododendrons was not less wonderful; in the shady woods of oak and beech of Headfort large and small specimens raised from seeds collected in Burma, China, Tibet and India are to be seen growing luxuriantly. His horticultural tastes were wide. He grew many plants of many other genera with success. Lilies of many different species, and the difficult, and still little known, genus

Nomocharis were among other plants for which Headfort Gardens were famous. Many rare and beautiful shrubs and deciduous trees are to be seen in many parts of the grounds, on sheltered walls, and other selected positions. The late Marquess was an enthusiastic and generous supporter of the Royal Botanic Gardens, Glasnevin, Dublin, and did much to enrich the national collection. His example, enthusiasm and generosity have encouraged others to build up collections and keep arboriculture and horticulture flourishing in Ireland. Lord Headfort was a noted shot, a yachtsman, and a clever photographer. He was a great lover of music. In 1901 he married Miss Rose Boote, and leaves two sons and one daughter. In 1930 he became a Fellow of the Linnean Society and in 1940 he received the Victorian Medal of Honour from the Royal Horticultural Society.

The many awards bestowed on plants from Headfort is an indication of the richness of the collection there; the pages of the 'Botanical Magazine' are the most eloquent testimony of the quality of the specimens and the discrimination shown in their selection and cultivation. Nearly 100 plates have been published from plants grown at Headfort, and there are still some unpublished.

Lord Headfort's death is a great loss to horticulture in Great Britain and Ireland.

F. W. MOORE.

BY the death of EDWARD HERON-ALLEN the Society loses one of its benefactors. He was a former Fellow, having been elected on 2 June 1892, but he resigned on 24 May 1929. It can now be revealed, however, that he was the anonymous founder in 1926 of the E. A. Minchin Fellowship, which perpetuates the memory of his old friend Prof. Minchin, the protozoologist.

The son of a leading solicitor, Heron-Allen was born in London on 17 December 1861, and he was admitted Solicitor of the Supreme Court in 1884, although he did not join the family firm until 1889. His ability and success were such that, when he retired from active practice in 1911, he had won for himself a high place in legal circles. In his capacity as solicitor, he rendered important service in 1914 in interpreting the wishes of the late Sir John Murray with regard to the disposal of the latter's natural history collections.

The responsibilities of his professional position did not by any means preclude other activities. Microscopy and especially the study of foraminifera were his main hobbies, and in his retirement they dominated his time. His interest had been stimulated in them while at school at Harrow, and in 1894 he published his first work on foraminifera, 'Prolegomena towards the Study of the Chalk Foraminifera . . .', a very useful guide to the student. Acquiring an estate at Selsey in 1906, Heron-Allen collected the foraminifera, recent and fossil, of the local shore sands, which, at the suggestion of F. W. Millett, he worked out with Mr. Arthur Earland. Thus were laid down the foundations of a close partnership which lasted till 1933, and which yielded in the intervening quarter of a century a large series of papers bearing on faunas from all over the world. In addition to British foraminifera (e.g., Selsey, North Sea, Clare Island, western coast of Scotland *, south Cornwall,

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* Published in the Society's Transactions, 2 (Zoology), XXI, 1916, pp. 197–300, pls. 39–43.

Plymouth), Heron-Allen and Earland brought within their ambit more distant faunas, such as those of the Gulf of Ajaccio, the South Atlantic, the regions visited by the *Terra Nova* and *Discovery* Expeditions, Lord Howe Island, and the Kerimba Archipelago, Portuguese East Africa. In many ways their report on the last-named (Trans. Zool. Soc. Lond., **xx**, 1914–15) was their most important work, with its re-determination of several of the specimens and species originally described by d'Orbigny in 1826 from Madagascar and Mauritius, and its first records of certain northern forms in tropical seas and of a number of species previously known only from the eastern side of the Indian Ocean. Heron-Allen and Earland also gave some attention to fossil foraminifera, and they published their investigations into those of the Eocene of Biarritz (1919) and the Miocene of Moorabool, Victoria, Australia (1924). Heron-Allen assembled a unique, comprehensive library on the group, and this, together with the magnificent collection of foraminifera which the work of the two collaborators brought together at Selsey from all parts of the world, was later transferred to the British Museum (Natural History) and presented to its Trustees by Heron-Allen in 1925 and 1926 respectively.

Two earlier workers won the admiration of Heron-Allen, namely, Alcide d'Orbigny and H. B. Brady. He visited France and the French museums to unravel the history of the great French naturalist of a century ago and to investigate his collections, and he paid tribute to his memory by devoting to him his Presidential Address to the Royal Microscopical Society in 1917. Brady's magnificent 'Challenger' Report was the basis of the systematic classification used by Heron-Allen, and he was more than impatient of anything which he construed as reflecting on the perfection of that great work—even though it were the result of later knowledge. Thus for many years he chafed at the numerous new genera and species introduced by oil palaeontologists, though he became more reconciled to them in his last years, when he understood some of the methods, problems and successes of workers on micropalaeontology in the search for petroleum. He welcomed anyone interested in foraminifera to the room given over to him and Earland at the British Museum (Natural History), and freely put at their disposal his library and collections.

Heron-Allen observed the ways of living foraminifera in aquaria at his Selsey home, and so came to propound his theories on their bionomics, and especially on purpose and intelligence in them, the basis of more than one address to various societies and a favourite lecture of his. In 1919 he was elected a Fellow of the Royal Society, and he was President of the Royal Microscopical Society from 1916 to 1918.

Heron-Allen found time beyond all this for other pursuits. An experimental horticulturist, he was an expert on the culture of asparagus, of which he produced a new strain. His wide knowledge of auriculas was recognized by his being made President of the National Auricula Society in 1928. He was an authority on the Selsey region, particularly its archaeology and history, and in 1911 he published a sumptuously produced volume on 'Selsey Bill: Historic and Pre-Historic'. He also wrote on its geology.

While a boy Heron-Allen's talent for the violin was developed and it remained a source of pleasure all his life. He thoroughly learnt the practical construction of the instrument, so that his book on violin-making (1882) bears the stamp of his own experience. He assiduously studied the bibliography and history of the violin, and wrote several articles on them, mainly from 1882 to 1896, but his last contribution, 'De Fidiculis Opuscula, IX, The Nefer Sign', appeared as recently as 1941. In addition he was an accomplished linguist, with a flair for the apt quotation from one or other of the classical or modern languages he knew well. He was justly proud of his knowledge of Persian, his mastery of which he showed in such publications as his translations of Omar Khayyám and of 'The Lament of Bábá Táhir'.

Of medium height, Heron-Allen was a striking figure in any company, both in earlier days with his clean-cut, good-looking features, and in old age with his massive, stooping shoulders and his rather long white hair. He was always an entertaining companion, and his wit could point a joke against himself. His dominating personality brooked no challenge, and his displeasure was unmistakably and openly expressed. But to his friends he was a wise and generous counsellor, and for them he would spare himself no pains. He used his wealth, too, to further those causes he had at heart, and he personally bore the expense of many of the plates illustrating his papers with Earland, such as those of their report on the foraminifera of Lord Howe Island, South Pacific, published in the Society's Journal, vol. XXXV, no. 238; 1924. Heron-Allen also contributed to defraying the expenses of the Great Barrier Reef Expedition of 1928–29.

He was twice married, first to Marianna, daughter of Rudolf Lehmann, the portrait painter, and sister of Madam Liza Lehmann, the singer and composer; and secondly to Edith Pepler, daughter of Dr. W. B. Pepler, by whom he had two daughters. He never got over the shock of the tragic death of his younger daughter in a motor-car accident in 1930 when she was on the threshold of a promising zoological career, and gradually, though at first imperceptibly, the old zest for his many interests faded. Nevertheless, even in his declining years, Heron-Allen was too vital and vigorous not to get a lot of enjoyment and entertainment out of life. In the autumn of 1941, however, he was seriously ill with pneumonia, and, though he recovered, it left its mark. He died at his Selsey home on 28 March 1943, and was soon followed by his wife. One daughter survives them both. H. DIGHTON THOMAS.

EINAR LÖNNBERG.—It has been truly said, 'Since the time of Linnaeus hardly any zoologist has known so much about the animal kingdom as Lönnberg'. Stalwart, dignified and refined in appearance, Lönnberg looked what he was—a leader of men. Any austerity in his expression vanished with his charming smile and affable tact in discussion or conversation. As Dr. P. R. Lowe wrote in 'The Ibis' (July 1943, p. 353), 'Lönnberg was beloved as a man and honoured as a zoologist'.

Axel Johan Einar Lönnberg was born in Stockholm on 24 December 1865, and died in the same city on 21 November 1942 at the age of 76. He was the sixth child of Dr. C. J. L. Lönnberg, himself a graduate of

Upsala, a landowner of East Gothland, interested in botany and arboriculture, and a member of the Swedish Parliament.

In 1884, the young Lönnberg left school in Norrköping, East Gothland, and proceeded to Upsala University, where he received the degree of Doctor of Science in 1891 on a thesis on the anatomy of certain tapeworms. During 1891–1903 he was an Inspector in the Swedish Government Fisheries Department. After some months in the Natural History Department of the Museum at Gothenburg, he was appointed in 1904 Professor and Chief of the Vertebrate Department of the Royal Natural History Museum at Stockholm; this appointmen the held for 29 years, retiring on pension in 1933, but continuing at the museum as a voluntary worker until his death in 1942. Latterly, when free of administrative work, he was able to divide his time between Stockholm and his 'sea-side home' at Kristinebergs, where there was a marine biological station, of which he was 'prefect'. He was a born lover of nature. His physical energy was equal to his mental acumen, and he seized every opportunity that he could to extend his knowledge, by foreign travel and by personally collecting specimens for the Swedish National Museum. Besides his many journeys in Europe, he visited Florida in 1892–3, crossing the Atlantic in a small schooner, in 1899 the country round the Caspian Sea, and in 1910–11 British East Africa.

The discipline of his earlier work on the anatomy of several groups of invertebrate animals was of real value to Lönnberg, and so to his students and disciples in his later researches on vertebrates, and without doubt helped to lay the sure foundations on which his opinions of broad zoological questions were built. In 1906 he founded the now well-known Swedish scientific journal 'Fauna och Flora', and edited it up to 1942. Besides zoology, Lönnberg took great interest in some branches of bio-chemistry, and did important original work, especially in the occurrence of certain colour substances in birds, fishes and some groups of invertebrates. Another, and very practical, side of his activities was museum work, both the proper exhibition of specimens to the public and the arrangement of material for the scientific researches of specialists. As a small example of his thoughtfulness for the men employed under him it may be mentioned that in the new museum building in Stockholm he had accommodation provided, where those of the staff who came in from a distance, bringing their own provisions from their homes and gardens, could have their food cooked on the premises. Yet another sphere of his life work was the protection and preservation of wild animals and plants, for the necessity of which he could speak with no uncertain voice. This difficult endeavour was aided by the high personal esteem in which he was held by the Government and by private individuals.

Lönnberg's knowledge of European languages in general, and of the English language in particular, was a great help to everyone at International „Congresses and Committees. He was a member of the Permanent Committee of the International Zoological Congress from 1927 to 1935 at least. At the Tenth Congress, held at Budapest during September 1927, he represented the Government of Sweden and the Swedish Academy of Science, and was elected a Vice-President of the

Congress. He attended the Fourth International Ornithological Congress in London in 1905 and the Fifth in Berlin in 1910. At the Sixth International Ornithological Congress, held at Copenhagen in May 1926, Lönnberg was chosen to return thanks to the Danish Ornithological Society on behalf of all the visiting foreigners. It might have been, in some ways, a difficult reunion, the first since the Berlin Congress of 1910, but Lönnberg made a useful and tactful speech, using the English language, and bringing in appropriately one of the wonderful fairy-tales of the famous Danish author, Hans Christian Andersen, with the application to that meeting, ' we are all united by the love of science, which is elevated above all politics '. It was also at this Congress that he read his important paper, ' On the origin of the North American fauna '.

The Seventh International Ornithological Congress was held at Amsterdam in June 1930; Lönnberg was President, and a general feeling of cordiality and friendliness prevailed the whole time. He made a remarkably good opening speech in English, recalling that they were meeting on classical ground, ' how, during the 17th and 18th centuries, students flocked to the glorious Dutch Universities to accomplish their learning and to obtain their degrees '. Among those young students were Linnaeus and his friend Artedi. ' These two young men were received with great friendliness, and thanks to this they could develop as they did, and lay the foundations of modern natural history '. This presidential address was a noteworthy occasion. Although chiefly concerned with ornithology, and addressed, in the first place, to ornithologists, Lönnberg spoke on many important subjects of interest to all zoologists. From the points of good advice given in this lecture emphasis should be placed on the following sentences :—' Above all one must avoid to be dogmatical. It must always be a matter of tact and taste to decide about certain cases. Nomenclature and terms are only the means, not the aim, and they are, and probably must be, more or less arbitrary '

After the Seventh International Ornithological Congress a Permanent Executive Commitee was elected, and Lönnberg was chosen as one of the five representative members to serve till 1934. When the Eighth Congress met at Oxford in July 1934, three Vice-Presidents were elected, namely, Graf Murany (better known as King Ferdinand of Bulgaria), Admiral Hubert Lynes and Lönnberg ; it shows the high esteem in which he was held by the ornithologists of the world. At the dinner in the Hall of Christ Church, on 5 July, it was Lönnberg who responded on behalf of ' the migrants, our Guests ', to the toast proposed in a very apt speech by Mr. H. F. Witherby. Lönnberg gave two papers to the Oxford meeting : ' The occurrence and importance of carotenoid substances in birds ' and ' Notes on the migration of Swedish birds '.

Lönnberg was a member of Council of the Linnean Society of Sweden for about 25 years, from its foundation in 1917 until his death. He was elected a Foreign Member of the Zoological Society of London in 1910, an Honorary Member of the British Ornithologists' Union in 1922 and a Foreign Member of the Linnean Society of London in 1928. In 1893 he brought back from Florida, not only extensive collections of natural history specimens, but also his Swedish-born bride, Eva Fries, of the family of botanic fame. Like her husband, this talented lady was thoroughly at home in the English language, and had many friends.

Zoologists in England grieve for the loss of, but are happy to have known, a man of such wide knowledge and kindly sympathies as Lönnberg, a man who was ever ready to give his valuable time to help solve any question of natural history, to listen to another man's opinions, and to argue debatable points in the greatest good humour and friendly co-operation. STANLEY S. FLOWER.

JOHN GRAHAM MURRAY, who became a Fellow in 1911, died suddenly at his home at Reepham, Lincoln, on 8 March 1943 at the age of 64. He was a native of Kippin, Stirlingshire, and on leaving school began his career as a gardener in Fifeshire, subsequently being employed in the Glasgow Botanic Garden. Thence in July 1900 he went to the University Botanic Garden, Cambridge, where, under Irwin Lynch, he remained until February 1903, going then as a 'young gardener' to the Royal Botanic Gardens, Kew, where he was employed until August 1904. He had made good use of his opportunities for obtaining not only technical proficiency in gardening but also botanical knowledge, and on leaving Kew he was appointed Horticultural Instructor for the Counties of Cumberland and Westmorland, being stationed at Carlisle, the work there being more or less under the auspices of Durham University. This post he held for some years until, in February 1909, he was appointed Organizing Instructor in Rural Economy, Nature Study and School Gardening in the County of Lindsey, with headquarters at Lincoln; but his work there was interrupted by four years' service in the Army during the Great War, part of which time was spent in Mesopotamia. On his return he became Chief Horticultural Officer for the County of Lindsey, a post he held until his death. He had intended to retire, but the onset of the present war found him ready to continue his work, with the added responsibilities which the activities of the Lindsey War Agricultural Executive Committee imposed upon him as Horticultural Officer. He took part in all the horticultural work of his large district, where he was responsible for about 100 school gardens, lectures, variety trials, model orchards, demonstrations and general advisory work. He often acted as judge at the local horticultural shows, and was active in the educational schemes of horticultural and allotment associations in the county, and, further, encouraged experimental investigations into some of the local horticultural problems, publishing also one or two reports on investigations carried out in the county, e.g. on the effect of coal-gas on plants and on the effect of source of seed-tubers upon the yield of the potato. His services were greatly valued in his county, but his enthusiasm for education carried him beyond the county limits. He had great visions of the part the new Central Schools might and should play in the life of the community, was constantly advocating the provision of refresher courses for those who held positions like his own, was a severe, though perhaps not always a discriminating, critic of the activities of various educational bodies, and always ready with his help and advice to further the advancement of promising and deserving young horticulturists. He was elected Chairman of the Horticultural Education Association for 1921–2, and frequently acted as examiner for the various examinations carried out by the Royal Horticultural Society, including the important professional examinations for the National Diploma in Horticulture (N.D.H.), and he enjoyed this work as a means of furthering the education of future gardeners. From 1932 onwards he undertook the duties of Executive Officer in connection with the schemes of the Society of Friends for supplying seeds, tools and so on to unemployed allotment-holders and for the settlement of unemployed men on the land at two centres in Lindsey. He combined a very active life in his profession with a genuine interest in plants and their ways, and leaves behind him the memory of an official whose services were very highly appreciated. He was buried at Reepham, where he had lived so long, his wife and daughter surviving him. F. J. CHITTENDEN.

RICHARD SANDERS ROGERS, the leading authority in Australia on the Orchidaceae, died at Adelaide on 28 March 1942 at the age of 80. He was elected F.L.S. in 1924. Born in Adelaide, he graduated B.A. at the young university there in 1883. Among his teachers were Sir Horace Lamb, Sir Edward C. Stirling and Ralph Tate, Professor of Natural Science, from whom he first learnt botany.

After graduation he went to Edinburgh to study medicine; there was then no medical school at Adelaide. He obtained the Edinburgh M.B., Ch.M. in 1887, proceeding to the M.D. in 1896, when he returned to Adelaide and settled in practice. At one time he was a consulting physician at the Adelaide Hospital, and for 26 years lecturer in Forensic Medicine at the University.

Rogers was a public-spirited citizen with a high sense of civic duty. In particular he gave much time to the State Medical Services, serving as Deputy Chairman of the Hospital Board. Mental disease interested him: he served on the staff of the Enfield Receiving House and the Mental Hospital. He published ‘A Medical Survey of the Feeble Minded in South Australia’.

He served in the field with the South Australian contingent in the Boer War, and in the War of 1914–18 he was Lieut.-Colonel commanding No. 7 Australian General Hospital in Adelaide. A list of Rogers' public services would be too long to give here, but reference must be made to his association for 44 years with the Board of the Public Library, Museum and Art Gallery of South Australia, of which he was Chairman 1929–31. He did particularly valuable service for the Public Library, especially on the scientific side, for he was always ready to secure the purchase of books, or even periodicals, which would be useful to students. When the Chair of Botany was founded at Adelaide in 1912, he was instrumental in starting and in securing long back-runs of several journals to supplement the inevitable limitations of the University Library. The result was that Adelaide is unusually well supplied with botanical periodicals.

Rogers' knowledge of field botany probably owed a good deal to his former teacher, Tate. He became specially interested in the terrestrial orchids which make a remarkable display in the Adelaide Hills in late winter and spring. His first publication was in the 'Transactions' of the South Australian Royal Society in 1906 on a new species of *Caladenia*. In all he published 27 papers in that journal, as well as many others with the kindred societies of other States. Species making, as such, was not his primary interest, though when necessary he was prepared to 'split', and he described 66 new species of orchids for Australia. The biology of the orchids, and especially their pollination, was always a great interest. He was most generous with his advice and help to all workers in other Australian States, perfectly willing to leave them the credit of making the new species. Probably one of the most remarkable of his discoveries was *Rhizanthella Gardneri*, which appears to be a wholly subterranean saprophyte, only discovered in the course of agricultural operations in Western Australia.

Rogers contributed the account of the Orchidaceae to the 'Flora of South Australia' by J. M. Black, A.L.S. This account, in 44 pages, is a good example of his care and attention to detail in drafting diagnoses. In 1932 he was President of Section M (Botany) at the Australian and New Zealand Association meeting in Sydney. His address, on 'Some Developments in Orchidology', shows his wide knowledge and depth of interest in the orchids of the Australian Flora. This address formed the basis of his thesis for the degree of D.Sc., which he submitted to the University of Adelaide at the age of 74 years. At the time of his death he was the senior living graduate of that University.

Rogers had a remarkable herbarium of Australian orchids. It was the more valuable because accompanying it were life-size water-colour drawings of every species and magnified dissections of the critical parts. These were the work of a professional artist, Miss R. Fiveash, whom he carefully trained and whose every drawing he lovingly supervised and directed. These have never been published in colour, and the half-tone reproductions of a few in the 'Flora of South Australia' give no adequate impression of their beauty and accuracy. We may be sure that so public-spirited a citizen as Rogers will have made careful plans for their preservation and use by students.

No reference to Rogers' orchid work would be complete without reference to his wife, Jean Scott Paterson, whom he married at Edinburgh in 1887 and who fully shared his enthusiasm for the orchids. She had a remarkable eye for plants in the field. A collecting trip with Dr. and Mrs. Rogers to some carefully chosen site in the Adelaide Hills, preferably in the spring following a bush fire, was an experience never to be forgotten.

T. G. B. OSBORN.

FRED STOKER, M.B., B.S., F.R.C.S., F.L.S., formerly of Wimpole Street, London, a well-known consulting physician, died at Loughton, Essex, on 20 July 1943.

He was for long interested in gardening and botany, and, after retiring from practice, he devoted his time to their study. He was elected a Fellow of the Linnean Society in 1918 and served on the Council from 1936 to 1940, becoming a Vice-President in 1938 and 1939. He applied his scientific mind to gardening and the problems of cultivation among the more difficult garden plants. He was particularly interested in ericaceous plants, especially the smaller growing ericaceous shrubs, and published in 1934 'Shrubs for the Rock Garden', which is considered one of the best works on this subject. He was also greatly attracted to lilies, which were grown with great success in his delightful garden at Loughton. He was one of the original members of the Lily Committee of the Royal Horticultural Society, and made valuable contributions to the knowledge of these plants by his papers on 'The Contractile Roots of Lilies', 'The Carniolicum Group of Lilies', 'European Lilies of the Isolirion Section' and other papers. His list of Lily names and Synonyms, published in the 'R.H.S. Lily Year-Book', will remain a very valuable contribution to the nomenclature of lilies. In recognition of his work for horticulture the Council of the R.H.S. bestowed on him the Victoria Medal of Honour in 1937.

Fred Stoker was the kindliest of men, and his enthusiasm was infectious to all who came in contact with him. His garden at Loughton, which was tended with so much love and care by his wife and himself, was a centre for all keen gardeners, young and old. He had a great fondness for animals and liked his visitors to see the squirrels which frequented his garden and even his house, and also the robins who one day, greatly to his delight, were accompanied by a young cuckoo they had brought up.

F. C. STERN.

JOHN SCOTT THOMSON was born on 30 June 1882 in Dunedin, South Island, New Zealand, where he passed the whole of his life, taking up the position of chemist in the widely known firm of Thomsons', Ltd., founded by his father. In his younger days an ardent footballer, and later a keen mountaineer, he became well fitted for what became his dominant interest, the collection, cultivation and study of the indigenous plants of the mountain regions.

His garden, devoted exclusively to the indigenous plants of New Zealand, became stored with a wonderful array of species of both scientific and horticultural interest. Remarkably successful with difficult subjects, he was the first to demonstrate how to grow with full success plants of the subalpine screes. He delighted in welcoming visiting botanists, especially those of other countries, and discussing his treasures and the botanical problems they raised. The award of the Loder Cup, in 1936, was a prized and well-deserved honour, as was his election as Honorary Fellow of the Royal New Zealand Institute of Horticulture.

With his life-long comrade, Mr. George Simpson, under the influence of Leonard Cockayne he became an active botanical worker, and together they published papers of merit and importance. These papers ranged over many subjects: forest ecology, wild hybrids, soil conditions, systematics and cultivation. Well known abroad, as well as in New Zealand, is especially their 'Vegetation of the South Island, New Zealand', written in collaboration with Cockayne for the 'Vegetationsbilder' series. This paper also shows his skill as a field photographer, as does 'Some Characteristic South Island Mountain Plants' ('N.Z. Alpine Journal', vol. VII, 1938).

His death in April 1943 made a serious gap in the list of amateur field botanists in New Zealand. All field botanists in this country, young and old alike, have lost a great friend and helper. H. H. ALLAN.

ADDITIONS AND DONATIONS

TO THE

LIBRARY

1942–3

Note.—Names of donors are given in square brackets. Separate copies of papers which are included in periodicals received by the Library are no longer catalogued.

Armstrong, E. A. Bird Display. Pp. xvi+381. 8vo. *Cambridge*, 1942.

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Butt, F. H. *See* **Johannsen, O. A.**

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Darlington, C. D. Recent advances in Cytology. Ed. 2. Pp. xvi+671. 8vo. *London*, 1937.

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Vol. 21 (1941–2).

Phytoplankton Periodicity in Antarctic Surface Waters. By T. John Hart. Pp. 261–356.

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The Southern Stocks of Whalebone Whales. By N. A. Mackintosh. Pp. 197–300.

Fraenkel, G. S., & Gunn, D. L. The Orientation of Animals. Pp. viii+352. 8vo. *Oxford*, 1940. [Dr. E. S. Russell.]

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—— *See* **Bertalanffy, Ludwig v.**

Woodruff, L. L., *edited by*. The Development of the Sciences. Pp. 336. 8vo. *New Haven*, 1941. [The Publishers.]

BENEFACTIONS.

List *in accordance with Bye-Laws, Chap.* XVII, *Sect.* 1, *of all Donations of the amount or value of Twenty pounds and upwards, received during the past five years.*

1939

The Royal Society : Grant-in-aid of publications, £200.
The Percy Sladen Memorial Fund : Cost of printing and illustrating 'Transactions', 3rd ser., vol. i, part 1.

1940

The late Major J. R. G. Gwatkin : An extensive collection of paintings of flowering plants, mainly British.
The Royal Society : Grant-in-aid of publications, £100.
The Percy Sladen Memorial Fund : Cost of printing and illustrating 'Transactions', 3rd ser., vol. i, part 2.

1941

The late Mr. Francis Druce : (1) £200 for general purposes of the Society ; (2) a selection of books from his library, including some rare early botanical works.
Rockefeller Foundation : Donation in aid of publications, £100.
Carnegie Corporation of New York, $8,060, for the preparation of a photographic record of the collection and manuscripts of Carl Linnaeus.
The late Sir Arthur Evans : Portrait in oils of John Dionysius Ehret, F.R.S., by George James, A.R.A., 1767.

1942

Rockefeller Foundation : Donation in aid of publications, £200.
The Royal Society : Grant-in-aid of publications, £100.
India Office : Complete set of The Linnean Society of London's publications.

1943

Rockefeller Foundation : Donation in aid of publications, £100.
The Royal Society : Grant-in-aid of publications, £100.

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